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PRINCIPLES OF COMPARATIVE PSYCHOLOGY

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PRINCIPLES OF COMPARATIVE PSYCHOLOGY

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Preface

This book, initiated by Willard Caldwell, represents the combined efforts of a group of psychologists working in the field of animal study to present the data and the interpretations of those data in this fascinating area. The contributors were selected because they are themselves responsible for much of the research material brought together in the text. Each is an independent scholar in his own area and is thus best able to interpret the outcomes of experimental and theoretical studies in that area.

The authors have tried to incorporate recent findings without neglecting the standard, time-tested material to be expected in a book that proposes to survey the entire field. The following features of the text illustrate this effort: a new look at the old problem of innate behavior; the effects of early experience on the development of sensory and perceptual abilities; the added insight on neural mechanisms resulting from the application of recently developed techniques; new research trends in motivation; fresh evaluations of findings in the areas of social and abnormal behavior; the role of genetics in the analysis of behavior; an account of the contributions of European ethologists to comparative psychology; the study of many different species; and the inclusion of divergent theoretical points of view rather than the particular biases of the contributors and editors.

One broad objective throughout the editing of this book has been to create a book in comparative psychology rather than in animal psychology (comparative psychology being defined as the study of differences and similarities among species). If we have not entirely succeeded in achieving this objective, the difficulty of finding the necessary pertinent studies may be to blame.

A somewhat novel departure from recent textbooks in the field is the inclusion of a chapter on the problem of classification of behavior. In that chapter zoological taxonomy is compared with what some day will develop into a behavioral taxonomy. For a quick overview of experimental and theoretical trends both past and future, the reader will wish to consult the last two chapters of the text.

The book is designed to be more than a mere compilation of factual materials. Experimental findings are essential, but of equal, or greater, interest are the principles drawn from these findings. The references listed at the end of each chapter will direct the interested student to the original sources for a more detailed statement of the techniques and data on which the textual material is founded.

The editorial committee cannot express too warmly its thanks to those who have contributed the several chapters. The enthusiasm of these authors for the work and the care with which they carried out their assignments are responsible for whatever merit the book may have. The task they undertook encroached upon an already overcrowded schedule. Each contributor was given the privilege of developing his topic as he saw fit. Perhaps because they are all activated by the same *Zeitgeist*, their finished products called for little editorial revision.

Space does not permit the acknowledgment of all the people who directly or indirectly contributed to this project. In addition to our co-workers, we owe a debt of gratitude to Clifford T. Morgan, former Consulting Editor for this series, who has been a constant and ever-ready source of encouragement. We also wish to thank J. C. Dixon and W. B. Webb of the University of Florida for reading a part of the manuscript. And each contributor, we are sure, would wish to acknowledge the aid and support of various other individuals who assisted him. Specific acknowledgments for permission to use materials from outside sources accompany those materials in the text.

Rolland H. Waters
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CHAPTER 1

The Nature of Comparative Psychology

ANIMALS IN THE LABORATORY

The use of animals in psychological experimentation might well seem paradoxical to one not acquainted with the scope of contemporary psychology. "Why study animals?" is a question frequently asked of the psychologist. The question has especial significance for the comparative psychologist. It appears to raise the problem of the validity of his specific field of interest and study. Let us dispose of it at once.

The psychological study of animals can be justified on a number of different grounds ranging from the practical and applied to the abstract and theoretical. As the layman sees it, the results of animal study yield information that can be applied to the training of animals as household pets, as circus performers, or as hunting and working companions. Breland and Breland [4]* describe a number of trained animal acts they have developed for entertainment and advertising exhibits. "Priscilla the Fastidious Pig" was trained to turn on the radio, eat breakfast at a table, pick up dirty clothes and put them in a hamper, run a vacuum cleaner, select her favorite (her sponsor's) food, and take part in a quiz program. The possibilities of such application are so extensive that these writers advocate the recognition of a special field of applied animal psychology. In a somewhat similar vein, an entertaining monograph by Hediger [12] shows how the study of animals, both in their natural habitats and in laboratory settings, is of value for the care and maintenance of animal exhibits in zoological gardens.

On a professional level, the techniques and information yielded by animal study are being applied to problems of wildlife and natural-resource conservation. Smith and Geis [20], for example, describe a training program, carried out in a fish hatchery, as a result of which fingerling trout were able to survive in greater numbers when planted in open streams. Fields [8] describes a "light barrier," a string of electric lights, by which young salmon could be directed away from, or past, dams on their way downstream to the sea. Von Frisch [10] reports a number of experiments in which he was able, by training bees to seek out certain kinds of flowers, to raise the yield of red clover by as much as 40 per cent and the yield of honey by 50 per cent or more. These are but a few examples of the way the results of animal study are being turned to practical account.

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* Numbers in brackets denote references at the end of each chapter.

Both practical and theoretical considerations dictate the use of animals in the psychological laboratory. In this context, the animal is employed as a tool or instrument of research. Many problems of human behavior arise in which the solution demands some form of operational or environmental control to which the human organism cannot be submitted. This happens when problems concerning the role of different neurophysiological mechanisms require the surgical removal of, or injuries to, the nervous system. It likewise occurs when investigations call for the control of mating in studies of heredity, for the application of intense and painful stimuli, or for prolonged subjection to hunger, thirst, or other biological drives. Studies of the effects of early experience on later behavior require a more rigid control of environmental, dietary, training, and handling schedules than can be imposed on the human subject. The student is already familiar with the use of animals in the study of interplanetary space. In all these and similar instances, the animal is used as the instrument by which various conditions are tested and evaluated. Which animal form will be used in such studies is determined by such practical matters as its suitability for comparative purposes, its ability to maintain itself under laboratory conditions, its cost, and other expenses involved.

Finally, theoretical reasons justify the use of animals in psychological experimentation and study. These theoretical reasons and their implications are of major significance for the comparative psychologist. Although he is interested in knowing that the results of his work can be put to practical use, his own task is the less spectacular one of discovering the laws governing animal behavior. The remainder of the present chapter develops this theoretical task in some detail.

THE FIELD OF COMPARATIVE PSYCHOLOGY

An adequate description of the nature of comparative psychology must include a statement of its subject matter, its methods, its problems and aims, and its relations with other branches of science. Since comparative psychology is a special branch or field of psychology, it is no accident that its characterization reflects this familial tie. This is one reason for the different definitions of comparative psychology that are found in the literature. Thus when psychology was looked upon as the study of conscious processes or of mind, comparative psychology was defined as the study of the consciousness or mind of the infrahuman animal. This is an older view [23], but it has its more modern adherents. Bierens de Haan [3], for example, defines psychology as the science of psychic realities or psychic phenomena, whether found in human or animal subjects. As the concept of the subject matter of psychology shifted from consciousness to behavior, comparative psychology followed the trend and became a study of the behavior of the animal.

Subject Matter

Stated in its broadest terms, contemporary comparative psychology is that branch of psychological science that takes as its subject matter the behavior exhibited by the animal in adjusting to the internal and external pressures that impinge upon him. The categories into which this behavior is divided are labeled according to their counterparts in the behavior of the animal most familiar to the psychologist, Homo sapiens. Hence the technical literature of comparative psychology contains studies of unlearned behavior, sensory and perceptual capacities, motivation, reasoning, learning, emotional characteristics, social interaction and organization, individual differences, and abnormalities in the behavior of the animal.

The connotation of the term "behavior" as used by the psychologist is not easily stated. As has just been suggested, the term is used to refer to such activities as sensing, perceiving, thinking, learning, forgetting, feeling, emotion, and their combinations in the activites performed by all forms of animal life in the conduct and management of daily living. There are other activities carried on by living organisms which are of minor interest to the psychologist, comparative or otherwise. Among these are the reflexes, the respiratory, digestive, circulatory, and other vegetative or maintenance functions of primary concern to the physiologist. At times the psychologist may include studies of these functions in his research program. When he does so, however, he is primarily interested in them as conditions influencing, or as indexes of, some other bit of behavior whose study is his major concern.

It is difficult to separate those activities of interest to the psychologist from those of interest to the physiologist. The task becomes even more confusing when the term "behavior" is used by the physicist and the chemist to describe the movements of the atom, by the astronomer to describe the movements of the planets, by the botanist to describe the activities of plants, and so on. What are the criteria in terms of which such a classification can be made? What is it that characterizes the behavior that constitutes the subject matter of psychology; that distinguishes it from the behavior studied by other disciplines?

Different authorities approach this problem differently. Some will assert that the difference is to be found in the degree to which the act studied involves the entire animal. Those acts which involve the entire animal are grist for the psychologist's mill; those that represent only part processes—such as digestion and circulation—are the proper subject matter of physiology. This is not very satisfactory since it can be argued, with justice, that the vegetative functions do require the interdependent working of all parts of the animal's body.

Another attempt to separate the two classes suggests that the psychologist studies those responses that can be described in terms of the results obtained rather than in terms of the specific bodily structures concerned. For example, the psychologist studies the acts of learning, of perceiving, etc., the performances by which the individual adapts and adjusts to his environmental conditions. The psychologist is not so much interested in how the muscular system is involved in these performances as he is in the end accomplished or achieved. This distinction has some merit. It suggests that the characteristic of behavior of interest to the psychologist is its outcome, its result, not the detailed manner in which it is done. This is not to deny that the psychologist may direct his attention to a refined analysis of the act. He frequently does. But he does this only after he has identified the act as a psychological phenomenon, not before.

In another place [24], criteria formulated earlier by McDougall [16] and Tolman [21] have been brought together. These criteria classify that behavior of interest to psychologists in terms of characteristics inherent in the activity itself. Four such characteristics are proposed: behavior is (*a*) in part autonomous, the product of conditions within the organism; (*b*) persistent, tending to continue until some end or goal is reached; (*c*) variable, shifting and changing until some appropriate way to the goal is discovered; (*d*) docile, or trainable. These characteristics do not, by definition, limit behavior to animals nor to the entire rather than to a part of the animal. They are sufficiently flexible to justify the use of different methods. Naturalistic, laboratory, objective, and subjective techniques can be employed depending upon the particular problem and specimen under study. They do not restrict behavior to the upper end of the phylogenetic scale, i.e., to man, but permit the psychologist to study, as behavior, any act that exhibits these characteristics.

Some such concept of behavior is needed to give theoretical justification and support for the program of work that the comparative psychologist sets for himself. It might be well to emphasize that these last criteria complement the conception that the psychologist studies the acts of the organism that can best be described in terms of their achievement rather than in terms of the specific muscular or neurophysiological mechanisms involved.

An illustration will help clarify the distinctions just made. Some time ago Wickens [25] conditioned the human subject to lift his finger as a means of escaping an electric shock being passed through a grid upon which the finger lay. After this conditioned response had been established, the subject was instructed to turn his hand over and again place the finger on the grid. Now if the conditioned response were made, the subject would find that, instead of escaping the shock, he would be pressing his finger harder against the grid. Nothing like this happened. When the conditioned stimulus was presented, the subject flexed his finger instead of pressing it downward. This demonstrates that the act, "escape from shock," had been conditioned or learned rather than a specific muscular reaction. This behavioral phenomenon is illustrated in many learning situations. The specific muscular reaction by which an end is reached is often not the one exhibited later. One rarely repeats a performance, achieves some end or goal in precisely the same way, through the activation of the same muscular movement. As the old proverb has it, "There is more than one way to skin a cat." We learn to skin the cat, not to exercise a particular series of movements.

Let us summarize what we have been trying to say. The comparative psychologist studies the behavior exhibited by the organism in adjusting to his environment. This behavior can best be described as an act that achieves a certain result, not as a series of particular muscular or neurophysiological responses. The acts of interest to psychology are those that exhibit the properties of autonomy, persistence, variability, and docility. The acts which constitute the class called behavior may be selected from any place along the phylogenetic scale and may be examined by any feasible method, naturalistic, laboratory, objective, or subjective, depending upon the problem and animal form under study. Behavioral acts are investigated in order to discover the laws governing their appearance, their form, and their subsequent history.

Problems and Aims

At the theoretical level, in which the discovery of the principles of behavior is of paramount interest, the use of the infrahuman animal is thus abundantly justified. This search follows a number of different directions. It may be oriented toward the problem of the general dynamics of behavior, the determination of the conditions producing change and modification of behavior. Or the investigator's interest may be directed toward ontogenetic development, the relationship between behavior changes and the increasing age of the animal. Again, the problem may be one of phylogenetic development, the tracing of some particular form of behavior as related to the position of the animal on the phyletic scale. Finally, the dominant interest may be a more strictly comparative one. The research worker may be interested in comparing one animal form with another, in discovering similarities and differences in the behavior exhibited by representative samples of different phyla, genera, and species.

The variety of problems investigated in comparative psychology is so great as to make any classification of them an arbitrary procedure. However, such an attempt, imperfect as it may be, has the advantage of providing an overview of the entire field. For this purpose, one possible grouping is presented. It will be found that this grouping cuts across the boundary lines represented by the later chapters of the book. This is unavoidable when any attempt to establish broad classes of problems is made. These strictures in mind, we may group the problems in seven categories, starting with (1) the analysis of an animal's behavior repertoire. This task involves discovering and cataloguing the kinds or forms of behavior the animal exhibits. As will be seen later, this seems to be a problem area open especially to naturalistic observation. It may, however, be investigated in the laboratory as well. This analysis, to be of most scientific value, should be carried out on a representative sampling of different animal forms. When this analysis is complete, there would follow (2) the problem of comparing the different types of animals with respect to the likenesses and differences of the behavior observed. This is the central and primary problem of comparative psychology as it has been defined traditionally.

The other classical and contemporary problems of comparative psychology are derived from these first two. These include (3) the ontogenetic development of behavior, the way in which a specific item of behavior develops within the single individual and a comparison of this development in different animal groups; (4) the phylogenetic development of behavior, a study of the way a given segment of behavior changes as we move from one phylogenetic level to another; and (5) the social organization and relationships present in animal groups. Two additional, somewhat more recent problem areas are found in the current literature. One area concerns (6) the study of a particular kind of behavior, e.g., learning, without any attempt at drawing comparisons except by implication. The investigator is interested in discovering the conditions affecting this function and uses whatever animal is suitable for this purpose. The other area studies (7) the extent and causes of individual differences between animals belonging to the same species. Such grouping of problem areas gives no more than an indication of the wide variety of specific problems falling within each of the major categories. This will be amply attested by the remaining chapters of the text.

Methodologies

Comparative psychology employs the general method of observation as do all scientific disciplines. The observations are made, at least this is the ideal, in harmony with the scientific safeguards that have been found necessary for the collection and interpretation of the data obtained. This means, as one consequence, that today anecdotal materials, stories, and casual reports of animal behavior are not accepted as valid data. Such materials have not been collected under conditions acceptable to the modern scientist, although they may suggest questions and problems that are interesting and quite possibly valuable. It was in the interest of developing sounder scientific interpretations of observed animal behavior that Morgan [17] formulated the principle which came to be known as Morgan's canon. This principle had the immediate effect of discrediting the use of anecdotes and of introducing a new era of scientific interpretation. (See Chap. 13 for a more complete evaluation of the canon.)

The methods employed by contemporary comparative psychologists can be separated into two major groups, those of naturalistic observation and those making use of conventional laboratory procedures. The dividing line between them is somewhat arbitrary, since the naturalistic procedures, as will be shown, may involve certain general experimental techniques by which observations are made more exact, and the laboratory worker may likewise arrange conditions in such a way as to make somewhat naturalistic observations possible. Both types of methods possess unique advantages for an understanding of animal behavior. We shall examine each in turn.

The naturalistic method is characteristically employed in making field studies. In these studies the animal's behavior is observed in its natural habitat. Typically, the observer makes no attempt to control the general conditions under which the behavior takes place although he may occasionally introduce some special condition, as a type of independent or control variable. Except for the observed effect of these special conditions, the naturalistic method does not permit the determination of the precise stimulating conditions eliciting the behavior. This more precise study of the stimulating conditions lies, again typically, within the province of the laboratory methodology. On the other hand, the naturalistic method enables the scientist to observe the function of the behavior exhibited in the animal's life cycle, something the laboratory procedures cannot do. In other words, the molar behavioral phenomena observed by the naturalist are fractionated in and for laboratory study.

The separation of learned from unlearned features of behavior is not easily accomplished through naturalistic observation. Such an analysis can be done adequately only when laboratory conditions and restrictions are imposed on the animal. Chapter 9 on social behavior, read in conjunction with Chapter 11 on the genetics of behavior, for example, will illustrate the comparisons made here.

The major contributions of the naturalistic methodology can be summarized as follows: (*a*) it reveals what the animal does when left undisturbed in its natural surroundings; (*b*) it thus contributes significantly to the analysis of the animal's behavior repertoire; (*c*) it brings to light the functional significance of the behavior; (*d*) it furnishes problems and hypotheses for more detailed laboratory study.

The brevity of the above list is a poor indication of the value of naturalistic observation and study. This value is perhaps better indicated by the assertion made by many authorities that the conduct of laboratory studies should be preceded by extensive field studies, that the true significance and fruitfulness of laboratory studies is entirely determined by a thorough knowledge of the animal's behavior in its own habitat, surrounded by members of its own and alien species.

The description of the naturalistic method of investigation has given some indication of the methodology employed in laboratory studies. Any attempt to enumerate the wide variety of experimental techniques employed by the research worker in psychology would be pointless. The student will become familiar with many of these procedures through the reports contained in the later chapters of this text, in the technical literature, and during the course of his own research experience. A more feasible task for our present purpose is a general characterization of the laboratory method.

First, the particular form of the method, the specific techniques and types of apparatus employed, is a function of the problem under investigation and of the animal being used as the experimental subject. This is the reason for the almost endless variety of procedures described in the literature. Second, the method is one which permits the investigator to elicit the particular segment of behavior he has elected for study. Third, the method promotes discovery of the precise stimulating conditions that evoke and otherwise control this behavior. Fourth, the employment of the laboratory setting makes possible a more exact study of the ontogenetic development of behavior. Fifth, closely related to this last problem is the fact that the role of hereditary mechanisms in determining the form of behavior can more readily be isolated in the laboratory. Sixth, the observations made can be repeated under known and controlled conditions.

COMPARATIVE PSYCHOLOGY AND THE BIOLOGICAL SCIENCES

The comparison of the naturalistic and the laboratory methods of investigation given above should not be interpreted to mean that there is any fundamental conflict between the two. The impression gained should be, instead, that the two methodologies complement and support each other. Like the three blind men of Hindustan, each approach brings light to bear on different aspects of the same problem, the behavior of animals.

This will be shown in greater detail as we analyze the relations of comparative psychology to the biological sciences.

Comparative psychology, since it studies the behavior of organic forms, belongs to the family of biological science. It bears a closer relationship to some members of this group than it does to others. The term "comparative" suggests a close kinship to comparative anatomy, embryology, morphology, and physiology. These sciences make significant contributions to the field of comparative psychology. Differences in behavior are rather obviously the result of differences in morphology and anatomical structure; fish swim, monkeys swing from trees, some birds hop while others run. The genetics and innateness of behavior borrow from comparative embryology, and comparative physiology helps us understand the neurophysiological foundations of behavior. Comparative psychology differs from these disciplines in its subject matter and problems investigated, as has been indicated above. On the basis of these differences, comparative psychology is most closely allied with the more recently developed field of comparative ethology. A certain amount of theoretical discussion concerning this relationship, particularly as indicated by the term "comparative," justifies a closer look at the programs of comparative ethology and comparative psychology. This examination will also acquaint the student with some of the quarrels among comparative psychologists themselves. This should not disturb us. Out of such controversies comes a clearer conception of our field of interest.

The term "comparative" in comparative psychology does serve to remind us that the original intention of the early students of this field was to compare and contrast, to search for similarities and differences in the behavior of different genera and species along the phylogenetic scale [27]. The continued use of this term to refer to current research and literature has been criticized. The criticism is that practically no truly comparative studies are being made [14], that the investigators are restricting their researches to but a few species, and that no comparisons among even these few are being made [2]. Another way of putting the issue is to say that contemporary comparative psychologists are concerning themselves with one or more specific problems of behavioral adjustment and, for practical and theoretical reasons, are using infrahuman animals as experimental subjects. Even in those instances in which the study involves the use of different species, as when a chimpanzee is raised in a human environmental setting [11, 13], the critic is not satisfied. He argues that such studies are concerned only with gross behavioral differences and similarities; they do not make an analytic study of that behavior. It seems that the critic takes comparative anatomy as the model comparative psychology should follow. Just as the anatomist searches for homologous (similar with respect to origin), not merely analogous (similar in function), structures in different species, so should the comparative psychologist, if he wishes to merit that title, look for homologous units of behavior in the different species he examines.

The difficulties confronting the comparative psychologist, were he to follow this advice, are fairly obvious. The anatomist has reached his results after a relatively thorough and exhaustive study of a wide variety of genera and species. He has available objective techniques by which the anatomical details can be validly identified and measured. Embryological study enables him to determine the origin and development of the various bodily structures. To take a simple example, the bones of a representative of a given species are objectively quantifiable; they can be counted and a definite numerical label attached to the result. They can be weighed, measured, and chemically analyzed. Quantitative comparisons can then be made between specimens taken from different species. Were comparative psychology to follow this model, it would be faced with the task of compiling a catalogue of the behavior repertoire of each species before comparable comparisons could be made. Criteria for the identification of the specific items of behavior would be needed. Additional criteria would be required in order to establish the homologous character of behavior exhibited by different species. The animal's behavior, its concrete reactions, appear far from matching the quantitative definitiveness of its anatomical characteristics. Novel stimuli, internal or external, or a different arrangement of new or old stimuli, coupled with the perseverative effects of previous behavior, elicit different forms of behavior or modify the character of repeated performances. The various combinations and permutations of possible stimulating conditions (some of which we cannot know since they lie in the future) and their effect on the resulting responses make the task of a complete cataloguing of behavior almost, if not quite, insurmountable. But theoretically, until such a classification of behavior is established, our interspecies comparisons cannot be carried out in the manner demanded by the critic. This general problem of classifying behavior will be more thoroughly considered in the following chapter. Some of the above criticisms have been offered by students of ethology, whose program is considered next.

Comparative ethology, or simply ethology, is that branch of biological science which studies the life ways and habits of animals. Lorenz, Tinbergen, and Bierens de Haan in Europe; Russell and Darling in England and Scotland; and Carpenter, Nissen, and Schneirla in America would be considered ethologists on the basis of some of the investigations each has carried out. A brief characterization of the ethological program will show its relation to comparative psychology.

Ethological studies are typically field studies carried out under the procedures of naturalistic observation. Interesting examples are to be found in Lorenz's *King Solomon's Ring* [15], a fascinating study whose title reminds us of the Biblical story of King Solomon who was given a ring that enabled one to speak and understand bird language; in Schneirla's [19] study of the military ants of tropical America; and in Darling's [5] study of red deer in Scotland. Although at times some experimental techniques and devices may be employed, as is shown in a paper by Emlen [7], the description of them as field studies remains appropriate. The behavioral phenomena studied are usually the gross behavioral adjustments the organism makes to its natural environmental conditions. The attempt is to find out, first of all, what the animal does when free and unrestricted by any experimental or laboratory setting. The major problem seems to be the identification and description of unlearned or innate behavior. (This search is also illustrated in Social Behavior, Chapter 9.) Some attention is given to the development of behavior in the individual animal, and this gives some of the studies an ontogenetic flavor.

Some of the ethologist's studies are directed toward the morphology of behavior, a description of the form and component parts of a complex activity. This makes his work somewhat comparable to comparative anatomy and the biological science of morphology. The ethologist tends to believe that such a morphological analysis of behavior is essential as the foundation of comparative psychology, that it needs to be done first, and that, looked at in this light, ethology represents a truly comparative psychology. It is quite apparent that the program proposed is similar to that of the comparative anatomist in many respects and would require that the difficulties described above be overcome. At the present time it seems that the ethologists have laid out a program of work the implementation of which has just been started. At the moment, it may be questioned whether the ethologist has carried out comparative studies to any greater extent than has the laboratory worker, whose studies have been criticized on this ground.

The criticisms made of comparative psychology can be met in another way. It can be asserted, with some justification, that some comparisons are made by the contemporary comparative psychologist. When the rat, for example, is tested for visual discrimination, for ability to delay his responses, for his performance in a learning situation, and so on, data from human subjects, and frequently from other infrahuman subjects as well, are available with which comparisons can be and are made. An illustrative example is a study by Fink [9] in which man, pig, dog, chick, rat, cat, water turtles, and land tortoises were ranked in that order on the basis of their scores in learning a maze habit. A study of this sort illuminates both the possibilities and difficulties of comparative research. But even when no data are available or reported in an animal study, in the background, shadowy though that figure may be, stands some conception and understanding of the manner in which the human subject would meet and respond to that type of problem.

The phenomena of behavior are sufficiently varied and complex to provide "elbow room" for a great many different scientific disciplines. They offer a challenge to the physiologist, the neurologist, the anatomist, the embryologist, the ethologist, the sociologist, and to the specialists working in the different branches of psychology. None of these can claim to be *the* science of behavior but all contribute to it. The major differences among these various disciplines is not the subject matter, in so far as it includes behavior phenomena, or the scientific nature of their various methodologies. The significant differences are to be found in the types of problem attacked. To illustrate, the typical comparative psychologist comes into or approaches the field of animal behavior through a background of training and study in human psychology. This background has provided him with the skills and interest in investigating problems dealing with phenomena that have come to be called psychological, with learning, sensory processes, motivation, and with emotional and social behavior. As a consequence, we find the comparative psychologist studying the nature of these and related topics in his animal subjects. By way of contrast, the typical ethologist has had a background of training in the more traditionally biological areas of anatomy, physiology, embryology, ecology, and related areas. When he turns to a study of animal behavior, this background of interest and training finds expression in the study of the general environmental, ecological, and social adjustments achieved by his animal subjects. Thus both ethology and comparative psychology are alike in their subject matter; they differ in their typically characteristic methodologies, but differ most markedly in the type of problem investigated. The ethologist's results suggest laboratory problems for the comparative psychologist and vice versa. The later chapters will give evidence of this interchange.

Similar likenesses and differences can be shown between comparative psychology and the other behavioral sciences. Such comparisons serve to illustrate the way in which, through interstimulation and exchange of information, each separate behavioral science contributes to the common goal, an understanding of animal behavior from amoeba through man.

HISTORICAL ORIGINS OF COMPARATIVE PSYCHOLOGY

Historically, the most significant impetus to the establishment of comparative psychology was given by Darwin's [6] evolutionary hypothesis. As is well known, this hypothesis embodied the conception that the higher forms of animal life developed from more primitive or lower forms. All animals were viewed as occupying different positions along a single continuum. This way of interpreting the relations of different species of animals to each other means that many of the characteristics of both structure and function, of behavior, present in the so-called "higher type" of animal would also be found in the more primitive. These characteristics, as exhibited by the lower forms of animal life, would be less complex in comparison with their counterparts in the higher animals, but in other respects essentially similar. The process of learning in man, rat, and paramecium would be fundamentally the same and subserve the same function. Emotional reactions in man would be shown in prototypical form in infrahuman animals, and so on. In other words, differences in structure and behavior among different genera and species would be quantitatively different but qualitatively alike.* The formulation of this hypothesis led a number of investigators, following Darwin, to search for these qualitative similarities in different animal species. These early students lacked our modern experimental techniques and hence, as has already been said, relied on the anecdotal method for the collection of their data. Examples of this method and its resulting interpretations are represented by the work of Romanes [18]. The modern experimental period of comparative study dates its beginning from Morgan's [17] critique of the anecdotal method.

But stimulation to comparative study came from other sources. The general conception and advocacy of the comparative approach and methodology was formulated by Wundt. Probably independently of any influence from Darwin's work, Wundt laid out this procedure, although in a somewhat implicit manner, in his *Lectures on Human and Animal Psychology*, first published in German in 1863 [26]. He later demonstrated the use of the method in his *Völkerpsychologie*. In this latter work, Wundt utilized the contrast between primitive and more modern periods of man's social and cultural development as the basis for his estimation of the mental and intellectual advancement of the groups examined.

Earlier than either Darwin or Wundt, the medical and physiological sciences were making use of the animal for experimental purposes. The students in these disciplines quite evidently considered the animal sufficiently similar to man, structurally at least, to justify the generalization of the results from animal study to the human subject.

Again antedating this medical employment of animals, or possibly cotemporal with it, Aristotle [1] during Grecian times advocated the study of animals and might therefore be called the first animal psychologist. His interest was not, strictly speaking, in a truly comparative analysis. He assumed that all organic forms of life formed a continuum; he was thus an early evolutionist and consequently held that basic similarities existed all along the phyletic scale. This being so, the basic characteristics of any item of behavior could be observed as well in infrahuman as in human subjects. Some of the important theoretical formulations left by Aristotle will be presented in a later section of the text. The reliance upon empirical observation, championed by Aristotle, seems to have declined during the Middle Ages. It reappeared during and following the Renaissance and since that time it has been the cornerstone of all scientific advances.

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* Our account, since it deals with Darwin's contribution only, omits reference to emergent theories of evolution.

From Aristotle, man's interest in animals may be traced back to prehistoric man, who must have made some crude observational studies of the animal in order to capture him for food or to tame him as a companion and servant. In spite of this long past, a really comparative psychology is a mere infant whose life span covers approximately the century since Darwin's epoch-making theory. Glimpses of this history will be given in succeeding chapters. These will give some indication of the changes in theory and experimental methodology that have characterized comparative psychology. For a more complete statement of this history, the serious student will want to consult such other sources as Warden, Jenkins, and Warner's [22] classic volume.

SUMMARY

This chapter has presented comparative psychology as the study of behavior wherever exhibited along the phylogenetic scale, whether by the simplest or the most complex animal form. The major task is that of the discovery of basic principles, or laws, of that behavior. Such principles, when found, provide both an understanding of behavior and the basis upon which comparisons among phyla and species may be made. The concept of behavior as presented here is a broad and general one. More specific and concrete interpretations will be given in connection with each subsequent topic.

During the course of this chapter, scattered references have been made to the succeeding portions of the text. A broad grouping of the problem areas in which comparative psychology is interested has also been suggested. Although each of the following chapters will deal with some aspect of one or more of these areas, it may be that a more specific orientation to the remainder of the text will not be amiss. This orientation will take the form of a brief description of the topics with which the text is concerned.

One of the problems of any science is that of classifying its phenomena into more or less discrete categories. Some facets of this problem have been mentioned in the preceding pages. The second chapter considers this topic in a systematic fashion. It evaluates and compares different bases of classification, suggests methods by which the task can be carried to completion, and presents a possible ordering of behavior. It also examines the challenging and puzzling possibility of using behavioral criteria as the base for an ordering of the different phyla and species along the phylogenetic scale. The suggestion will be made that such an ordering would differ from that based on the criteria employed in zoological taxonomy.

The problem of classification disposed of, the text gets on with its main task, the study of animal behavior. The study begins with the behavioral mechanisms present at or soon after birth. This is followed by a survey and analysis of the sensory processes. Placing these chapters early in the text emphasizes the hypothesis that maturational and hereditary mechanisms are important determiners of behavioral development. Then, too, there is the obvious fact that sensory discrimination is basic to the acquisition of differential responses to the environment.

The development of complex behavior seems related to the presence of another set of conditions that come about as a fundamental property of living organisms, internal motivating conditions. Two approaches to this complex problem are represented in the text. The first (Chap. 5) is representative of the traditional, and most widely accepted, view that motivational psychology is based on the fundamental and primary biological drives. The treatment does not remain merely traditional, however, it "moves with the times" and presents an integration of the traditional and the more modern interpretations of this approach.

The second approach to motivation (Chap. 6) emphasizes the nonphysiological factors in motivation. That chapter treats those conditions of behavior that have customarily been referred to as the secondary, the derived, or the learned drives and motives. These two approaches present some differences in interpretation and terminology. The problems of motivation are complicated, and final answers are not available; hence different approaches to them are justified, even though the resulting suggested organizations of facts seem to show some lack of agreement.

The topics of learning, of the cognitive and higher mental processes, then follow as the major avenues through which the individual organism comes to exhibit complex forms of behavior. It will be clear that this development comes about as a result of the basic mechanisms of sensory, motor, and motivational equipment with which the organism begins.

The organism as a social unit, its behavior as dependent upon members of its own and alien species, is analyzed in Chapter 9. Here we see once again an illustration of the naturalistic method of study and of the problem of classification of behavior as exhibited in different forms of social behavior. The treatment and analysis of this topic have implications above and beyond the particular species examined, implications and suggestions for an understanding of behavior at the human level.

The havoc wrought by abnormalities of behavior and mental disease in our society, both for the individual and for the group, has led the comparative psychologist, as well as all behavior scientists, to an examination of these phenomena. Research studies in this area by the comparative psychologist involve the imposition of conditions of severe stress on the experimental subject and hence, as pointed out earlier, are illustrative of the use of the animal as an instrument or tool. Such investigations represent attempts to discover the etiological factors in abnormal behavior and to test the relative efficacy of different therapies. Chapter 10 brings the techniques and findings of such research efforts together.

The general procedure up to that point in the text is that of behavioral analysis. With Chapters 11 and 12, we turn to a genetic and neurophysiological analysis of the conditions of behavior. The topics covered in these two chapters might well have come earlier in the text. This relatively late treatment is justified, it is believed, on the grounds that it should await a prior analysis of behavioral phenomena at a more molar level. This prior analysis serves to guide and orient genetic and neurophysiological studies.

Throughout the history of comparative psychology, different comprehensive, as well as more restricted, theories have been developed and debated. The course of this development and the present status of different systematic and theoretical issues are sketched in Chapter 13. In many ways a study of this topic serves as a review and integration of the preceding materials in the text. This review, summary, and intepretation are continued in the final chapter. The writer of that chapter has attempted the difficult task of reviewing the past and the more hazardous task of predicting the future of research efforts to understand the behavior of man and animals.

Exciting adventures lie ahead for the student. It is our hope that he will find them challenging and invigorating.

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CHAPTER 2

Problems of Classification

In the opening chapter, comparative psychology was defined as the science concerned with similarities and differences of behavior among species. The study of these similarities and differences has been carried out by both psychologists and biologists, each group undertaking the study from slightly different viewpoints and each employing its own variations of the experimental and naturalistic methods. The mass of behavioral data accumulated has become enormous, and the question of how to organize and simplify it in the most meaningful way naturally arises. At this stage of development in any science, the principal mode of organization is achieved through the inductive process of classification. Once a stable system of classifying behavior has been achieved, a widely ramified deductive approach to behavior can be made.

Biology has its own inductive system (taxonomy), and it has long been the tradition in comparative psychology to use this zoological classification as a framework within which to arrange behavioral data. As will be described later, this practice has proved to be of limited value for comparative psychology. In contemporary thought on the subject, therefore, the practice has been questioned, and the suggestion has been made [15] that an analogous system could be developed for behavior.

The present chapter will consider the field of zoological taxonomy as an example of classification of immediate relevance to comparative psychology and evaluate the problems involved in establishing a similar system for the study of behavior.

ELEMENTS OF CLASSIFICATION

The essential element of all psychological studies is the naming and description of the population studied, whether it is a group of Wistar rats thirty to forty days of age or a population of adult, white, middle-class American men. In comparative psychology this necessity of naming and describing the population has been simplified by the efforts of zoologists, who have named and described 128,050 species of invertebrates other than insects, 850,000 species of insects, 20,000 species of fish, 6,000 species of amphibians and reptiles, 8,590 species of birds, and 3,200 species of mammals [13]. The names of these species, all in Latin binomials, immediately specify the morphological characteristics of the organism which is studied. The Latin binomial for the familiar laboratory rat, for example, is *Rattus norvegicus,* which specifies a rodent about 8 inches long, with a scaly tail about 6 inches long, weighing about 250 grams and having a hard palate extending posteriorly beyond the last molar [4]. In addition, these names indicate the phylogenetic relationship among closely related forms and enable remotely related organisms to be classified readily. Phylogenetic relationships are established by the evolutionary history of a species. For example, the Norway rat (*Rattus norvegicus*) is immediately recognized as a close relative of the black or Alexandrine rat (*Rattus rattus*) by the fact that the first Latin name (genus) is common to them both. The more remotely related house mouse (*Mus musculus*), however, is recognized as a closer relative of the Norway rat than it is of a wood rat (*Neotoma floridana*) because both the house mouse and domestic rat are classed in the same family (Muridae), while the wood rats are classed in a different family (Cricetidae). A description of this phylogenetic system of classification will be one undertaking of this section.

The classification of all species of animals has undergone a historical development which has culminated in a natural system based upon the evolutionary concepts of phylogeny. In order to fully appreciate the factors involved in modern zoological taxonomy and the problems involved in establishing an effective analogous system for behavior, it is necessary to consider what scientific classification is and what it accomplishes.

What Is Scientific Classification?

Classification has been defined as that process which achieves "the actual or ideal arrangement together of those [events in a series of events] which are alike and the separation of those which are unlike, the purpose of this arrangement being to disclose the correlations or laws of union of properties and circumstances" [8, p. 677]. Those systems of classification, such as the modern zoological system, are called natural or scientific which express the order of existing things as determined in nature.

Operationally, scientific classification is the process of organizing phenomena into kinds or classes. Phenomena are assigned membership in a particular class through the possession of some property or trait which is common to all.

Traits Are Basic in Classification. The process of scientific classification begins with phenomena possessing numerous traits or characteristics which can be described in a number of ways. Sometimes the same trait will be observed in a number of different phenomena. When this happens, the phenomena are said to resemble each other with respect to the trait. The resemblance can be of any sort, that is, based on any element, aspect, occurrence, function, structure, or process by which the phenomenon can be described. The isolation and definition of these descriptive traits is the first and primary step in the process of classification. These traits define and demarcate classes.

The essential requirement of a trait, in scientific classification, is that it be a property or characteristic of the phenomenon under study. Such traits may be one or the other of two general kinds. In some cases the traits chosen for use may be the visible or objectively specifiable aspects of a given event, e.g., the fact of doing a particular thing—pressing a bar, running through a door, or making a courtship response. In other cases, the traits chosen may be abstractions from a series of events. These abstractions are defined in terms of the objective aspects of the series, e.g., "learning" inferred from a series of bar pressings.

There are many traits which are consistently found together in nature, and it is with these that the scientist is chiefly concerned. When traits are observed to be so bound to each other that where one is the other is, and where one is not the other is not, they are said to be *correlated*. There seems to be no limit to the nature or number of these correlations. There may be correlations of material and structural elements, as albino hair and unpigmented retinae; correlated functional aspects, as when a poorly functioning cerebellum is associated with motor incoordination; and structural-functional relations, as when a short, stocky physique is correlated with slowness of movement. A recent trend in psychology is to correlate surgical operations of various sorts with behavior changes.

In classification, such correlations of traits are extremely important. If it were not for such correlations, we could not make any one arrangement which would enable us to treat all of the traits within a single system.

The Concept of Class. The concept of *class* is useful because it is readily observable in nature that groups of phenomena "go together" or are somehow related; i.e., they possess certain traits in common. Thus a class is a convenient grouping of phenomena which "go together." Individuals hold membership in a particular class because they possess a given trait, while other individuals not possessing this trait do not hold membership in that class. It is not necessary that the members of a class resemble each other in *all* possible ways but only in those ways which define the class. For example, if the trait which defines the class is "possession of hair," then it does not matter whether the individual moves by running or by swimming. If any individual has hair, it holds membership in that class.

Class definitions are not immutably fixed and static. Sometimes it is found that successive samples of a class may differ in some property after the class has been defined. For example, vertebral animals differ in many properties. When this occurs, the scientist assumes that the class needs refinement and, with further investigation, he will find the additional specifications for new subclasses or categories. When these specifications are taken into account, all the members of each of the new subclasses will have essentially the same properties. In Figure 2-1 the system shown might have started with a two-class system: those classes possessing trait *C* (i.e., hind limbs) and those classes not possessing trait *C*. Further investigation could have led to the development of the series shown when further differentiating traits were noted. This flexibility of classificatory systems is one of convenience; the revisions and refinements in the system are made only when it is necessary for a specific purpose and after the traits involved have been clearly established. Very often it will be found that the individuals of a class possess a number of traits in common, yet show minor differences from each other with respect to possession or nonpossession of one or more other traits. In this event, it is customary to set up a system of subclasses, using the several traits for establishing the new groups.

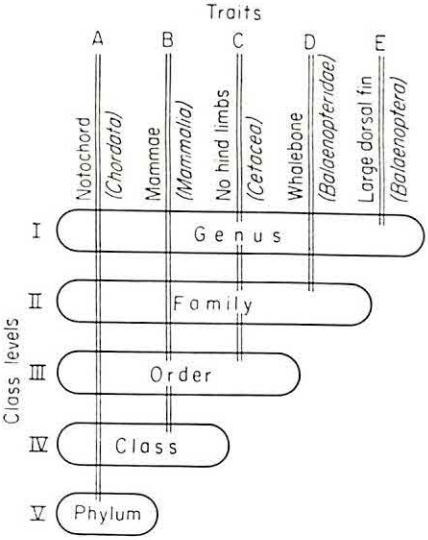

FIG. 2-1. A diagrammatic representation of linear classification, using the zoological classification of the finback whale (*Baloenoeptera physalus*). Any given trait indicates the class level of relationship which can be determined. ("Class" at class level IV is used as a technical zoological term.)

In arranging classes of phenomena into a system there is no absolute and correct mode to be followed, that arrangement being made which is most convenient and instructive for a particular purpose. The arrangement may be in tabular form (as in Mendeleev's table of chemical elements) or in linear form (as in the zoological classification of animals). The first arrangement assumes no special relation between the individual classes, while the second arrangement (often called the evolutionary or phylogenetic arrangement) assumes that all classes are related through descent from the original life germ. The linear arrangement is assumed to express this "line of descent." This is represented graphically in Figure 2-1, with the classification of baleen whales as an example. It will be noted in this diagram that trait *A* (i.e., notochord) is found at all five levels, trait *B* (i.e., mammae) at levels I through IV, etc. All five levels are related since each possesses

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trait A. Each class level differs from the class above or below it by the presence or absence of a single trait. This type of arrangement is commonly employed in zoological systems.

Criteria of Classification. Several criteria for classificatory schemes may be derived from the diagram in Figure 2-1. First, the system is exhaustive, i.e., it provides a class for each of the traits concerned. In the second place, such a scheme proceeds a step at a time, each step being taken with respect to a single trait which is concerned with that step only. Finally, the classes at a given level are mutually exclusive. If an animal falls into one class, it cannot at the same level fall into another class.

ZOOLOGICAL TAXONOMY

Zoological taxonomy furnishes an excellent example of how the principles of classification serve to order the animal kingdom and to provide testable hypotheses. The zoological system is also important for the comparative psychologist, since he uses this system to select animals for study.

The problem of classifying every animal species precisely is not yet solved because the origin of each species can be determined only by inference. Nevertheless, as a system, zoological taxonomy has endured for a century, providing not only standard names and categories for each animal, but also a source of new concepts about the origin and evolution of animals. Such a thoroughly tested system of classification may serve psychologists as an example in their efforts to organize and classify behavior. The concept of evolution, which is basic to the zoological system of classification, is probably not the concept most useful for a classification of behavior, nor will the problems encountered in the classification of animals and behavior be the same. Still, the experience gained in the classification of animals may guide the classification of behavior as it is being developed by psychologists.

System Used in Zoological Classification

As stated previously, classification consists of placing things in classes or categories and arranging the categories *in a systematic fashion.* The system used in zoology is a hierarchy with the highest, most general category encompassing all of those below it. The system incorporates the principle of *phylogeny,* the evolutionary history of a species (Fig. 2-2). The taxonomic position of each animal depends upon the number of ancestoral species it has in common with other animals. Animals with the most ancestors in common are more closely related than those with only a few. In human genealogies, which work on a similar principle, brothers are more closely related than cousins because brothers have both parents and grandparents in common, while cousins have only the same maternal or paternal grandparents in common. This phylogenetic system depends upon evolutionary concepts described by Darwin in 1859. In order to understand how phylogenetic relationships are established, we must first describe briefly the process of evolution. Following this description, we will return to an examination of the criteria used in zoological classification.

The Process of Organic Evolution

The change of an organism from one form to another during its evolution depends upon four processes: (*a*) variation, (*b*) isolation, (*c*) selection, and (*d*) random genetic drift. The first two processes are always necessary for evolution with the addition of either or both selection and random genetic drift.

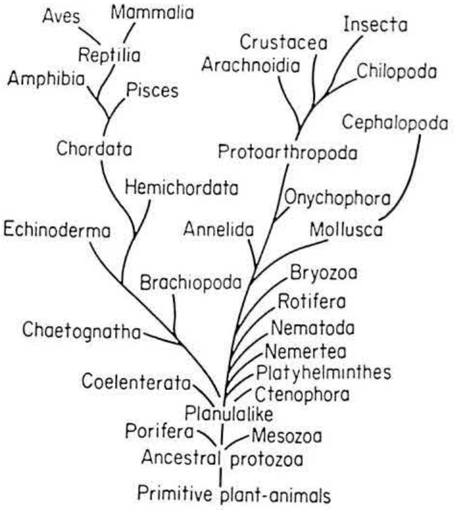


FIG. 2-2. A phylogenetic diagram or "tree" indicating the evolution of different forms of life from a common ancestor at each branching point. All animals arise from the ancestral primitive plant-animals. [*From W. C. Allee, De l'extrapolation en sociologie comparée. Scientia,* 1949, **60,** 67–74.]

Variation. The differences which are readily apparent between individuals of one species are called variations. Variations may be caused by such environmental factors as nutrition, experience, and exercise or by modifications in the germ plasm (genes and chromosomes) which affect the structure and function of all parts of the body. The *phenotype* of an individual refers to those characteristics which are exhibited in the body tissues, such as the color of the fur, the length of the body, the number of digits. The *genotype* of an individual refers to the number and kinds of genes and chromosomes in the nucleus of each cell. Only genotypic variation resulting from changes in the germ plasm, either as mutations or recombination of genes, can have an effect on evolution. Phenotypic variations may affect the individual expressing them, but they cannot be passed along to succeeding generations. The relative importance of mutation and recombination to evolution is difficult to assess. Certainly mutation is necessary to contribute new genes to a population, but the constant recombination of genes often provides for their most favorable expression.

Isolation. Mutations have little effect on a population if it is either very large or if it is continuously being swamped or diluted by animals bearing normal genes. Consequently, isolation is imperative to the evolution of a species. Probably most isolation is purely geographical [12]. A species may so extend its range that the populations at the extreme ends of the range become isolated from each other. Mountain ranges have arisen between a once continuous population, water has separated land animals, or changes in climate have created barriers of deserts, swamps, and ice floes. Mutations occurring in the extremities of the range or in the isolated ranges begin to have an effect not observed in the animals inhabiting the original range.

After geographical isolation has separated a single species long enough for it to diverge into two species, the previous barrier may be eliminated and the two new species come together again. Now the species may maintain their integrity by other types of isolation, without which the populations would interbreed and their differences would disappear. These other types of isolation may be physiological (infertility), ecological (occupy different habitats), seasonal (mate at different times of the year), mechanical (gross differences in size), and psychological (exhibit different patterns of mating behavior). A single species may thus become isolated and evolve differently in the separated ranges.

Selection. Selection refers to the process by which some animals are eliminated from the population or are otherwise prevented from passing on their genes to succeeding generations, while other animals remain as the progenitors of the subsequent populations. Selection of certain individuals for posterity may occur in a number of different ways. The two principal divisions are (*a*) artificial, in which human beings select desirable traits which are passed along to subsequent generations, and (*b*) natural, in which the natural forces eliminate some individuals and provide for others. The natural forces may be drought, excessive water, heat, cold, quantity and quality of food, available shelter, diseases, and predators. Some of these forces are independent of the inherent adaptability of the animal. For example, a flood may drown a large number of terrestrial animals regardless of their swimming ability. Only those individuals fortunate to be living above flood waters survive. In an excessively cold winter many insects hibernating in ordinarily suitable places may be destroyed. Only those insects hibernating in protected places live to reproduce. Other forces are more selective of the adaptations of particular individuals with a genetic mutation which enables them to survive such catastrophes as a severe epidemic. A mouse bearing genes for cryptic coloration of its fur may live to pass the genes on to its offspring, while a conspicuously colored mouse is eliminated by hawks and owls [6]. Consequently, selection may either eliminate large populations without discrimination for adaptiveness or it may work with remarkably fine precision by removing only the least adaptive from the population. Selection has evolutionary significance only when genetic characteristics are involved, although it may operate as well on nongenetic characteristics.

Genetic Drift. Genetic drift is one of the names applied to any random change of gene frequencies within a population. It may have the same effect as selection upon evolution, but it is purely random; and nonadaptive mutations may increase as well as decrease in frequency [7].

Such a process may explain the presence of nonadaptive features during the evolution of an organism. On the other hand, a change in the environment may later give the mutation, which has increased in frequency through chance, a survival advantage.

Interpretation of Phylogenetic Relationships

The numerous species we see on the earth today are products of a long evolutionary past, during which a parent species gave rise to new species and then became extinct. Among those animals that have left an abundant fossil record of their past, there are more extinct species known than there are living species. Most species became extinct without leaving descendants. Consequently, the recent (living) species have evolved from moderately few ancestoral species. Somewhere in their geological past, all recent species, then, have had a single or a few common ancestors. In closely related species, the common ancestor existed in recent geological periods, while distantly related species have their common origin in the remote geological past. Theoretically it should be possible to find the complete genealogy of all species; however, the scarcity of fossil forms has made this impossible. Even in the most complete fossil records there still are large gaps between early and late forms. Paleontology, therefore, cannot provide the lineage which will establish the relationship among *recent* species. This task has fallen to the taxonomist.

A phylogenetic interpretation of a similarity between species depends on whether the similar character was inherited from an ancestor with that character, homology; or whether the similar character was acquired independently from two different ancestors, convergence; or whether the similar character developed independently after genetic isolation arose between related animals, parallelism.

Homology. Homologous structures, functions, or behavioral patterns are derived from a common ancestor (Fig. 2-3). The forelimb structure of all mammals has apparently been derived from the common ancestral mammal. This appendage has evolved differently among most orders of mammals. In the primate, it has become a hand; in the perissodactyls, such as the horse, it has become a hoof; in bats, it has become a wing. Regardless of these apparent differences, the basic arrangement of radius, ulna, carpals, metacarpals, and the phalanges still bears evidence of their common origin. Superficial similarities which may later develop, such as the webbed feet of the otter and beaver, are not homologous because one developed from an ancestral carnivore and the other developed from an ancestral rodent. Homologous structures are only those which are drawn from a common pool of genes of the ancestral form. Usually animals with the greatest number of homologues are more closely related than those with only a few homologues. Thus, the wood rat (*Neotoma*) may resemble a laboratory rat (*Rattus*) more than it resembles a meadow mouse (*Microtus*), but is more closely related to the latter because the wood rat has at least one more homologous structure (tooth structure) in common with the meadow mouse than it has with the laboratory rat.

Similar patterns of behavior are sometimes interpreted as homologous simply because they arise in two closely related animals. Unless they are traced back to a common ancestral source, such an interpretation may lead to generalizations which are unwarranted. Frequently similar behavioral characteristics may be acquired independently from different ancestors, or even during the life of the animal under investigation. This problem will be discussed at length in a later section, after we first examine how similarities may arise by convergence and parallelism.

Convergence. Animals often develop similar characters independently during the course of their evolution (Fig. 2-3). This independent acquisition of similarities is known as convergence. Convergent similarities are unlike homologous similarities in that they are not derived from a common ancestor and are often modifications of different organs to serve the same function. For example, animals that have evolved wings to propel themselves in air, such as the bats, birds, and insects, have different structures to serve this function. The bats have skin stretched between metacarpal bones; birds have feathers arising from the skin surrounding the fused carpals and phalanges; and the insect wing develops from a membraneous fold in the body wall. Although the anterior appendages of bats and birds have homologous elements, their function as wings is convergent. The same elements may serve a host of different functions. Three orders of mammals have independently developed spines on their backs in species like the rodent porcupine, the monotreme echidna, and the insectivore hedgehog. Despite this superficial resemblance of spines, these three species have developed from different ancestors and are not closely related phylogenetically.

Parallelism. Parallelism is a third process which produces similarities in animals. Parallel characters are those which have evolved independently but similarly along two lines of descent (Fig. 2-3). It is frequently difficult to distinguish parallel from convergent evolution. Parallel characters usually develop in related animals which have been isolated from each other but have evolved in somewhat similar environments. On the other hand, convergent characters may appear sporadically throughout the animal kingdom. The Australian marsupials are frequently cited as an example of parallel evolution because they have long been isolated from the evolutionary currents of other mammals. As a result of this long period of isolation, the Australian marsupials evolved into families which sometimes resemble the placental orders of carnivores and rodents. The marsupial wolf, for example, resembles a carnivore wolf; however, this resemblance is only superficial because both wolves evolved these similar characteristics long after the marsupials were isolated on the island continent. In contrast to parallel characters, convergent characters usually arise as secondary modifications in animals which were initially quite different. Any aquatic animal that was derived from terrestrial ancestors usually illustrates convergence in the development of webbed feet. Consequently, webbed feet may be found as secondary adaptations in many different orders of mammals, such as the monotremes, insectivores, carnivores, and rodents.

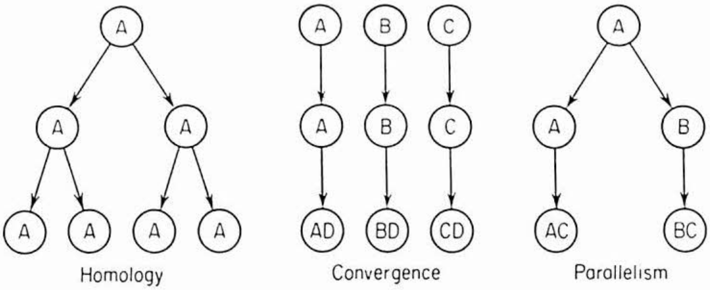


FIG. 2-3. Each circle represents a species bearing the trait indicated by a capital letter. In *homology*, the trait is passed from the common ancestor to all derived species. In *convergence*, each ancestor contributes its homologous traits, but a new trait (*D*) arises in later species. This trait may obscure the homologous traits and make the three species bearing trait *D* superficially resemble each other. In *parallelism*, one species replaces the homologous trait *A* with the new trait *B*, and both lines evolve under similar circumstances where trait *C* arises. Trait *C* may also obscure the homologous traits *A* and *B* by superficial resemblances.

Basis of Zoological Classification

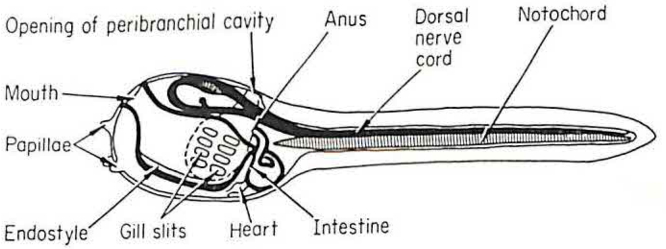
In the search for phylogenetic relationships, taxonomists have used the contributions from morphology, paleontology, embryology, physiology, genetics, zoogeography, and ethology (behavior). Although morphology has been employed in the study of taxonomy more than any other discipline, it alone is not sufficient to confirm a relationship when there is conflicting evidence from any of the other disciplines. Discrepancies among the various fields merely indicate our ignorance about the phylogeny of the organism under examination. Most relationships can be determined as our knowledge of the embryology, genetics, and behavior of the animal increases. Then the various pieces of information fit beautifully together and what had previously been a taxonomic enigma becomes an orderly mosaic.

Morphology. Morphological comparisons indicate relationships by means of the number of anatomical features two animals have in common or by the similarity of structure. In general, morphology alone presents an archetypal system of classification, where individuals with the most common characteristics are most closely related. However, this system is not always in accord with phylogeny. The marsupial wolf, previously mentioned, probably has more anatomical features in common with the carnivores than it does with the kangaroo. When such features are recognized as products of parallelism, rather than homologues, they are disregarded as a basis of classification and other features are sought.

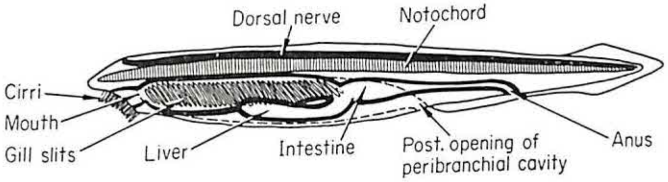
One reason for the preponderant use of morphological comparisons in taxonomy is the availability of the material. Animals from all over the world can be collected, preserved, and brought into museums where their anatomy can be closely examined. It is much more difficult to collect the data for physiological or genetic comparisons. Consequently, the first clues of a phylogenetic relationship are furnished by morphology. Because preservation of the structures used in taxonomy is important, the most easily preserved parts of animals are first studied. These parts may be the shells of mollusks, the chitinous exoskeleton of insects, the scales and bones of fish, the feathers, legs, and bills of birds, and the skulls and skins of mammals. Occasionally the hard parts of animals may be misleading, for if only the skeleton and skin of the marsupial wolf, previously mentioned, were studied, it could easily be classified with the carnivores. Upon the examination of such soft tissues as the uterus of the pregnant female, the absence of the placenta would immediately reveal that it was marsupial and thus related to the kangaroo.

Paleontology. Paleontology is the study of extinct animals by means of fossils, which have been preserved throughout the geological past until recent times. Although paleontology utilizes the anatomical features of animals, its contribution is unique. If we had a complete series of fossils for every species, it would be possible to trace the continuity of their descent from the original ancestor. It is like following the colored wires of an electrical circuit to their source, rather than guessing which wires came from the transformer, the condensers, and the relays by their color and size at one end. Such continuity is, of course, lacking in the fossil record. Instead, the abundance of living and extinct species with few fossil remnants of their immediate predecessors often complicates their phylogenetic relationships. In some species, however, the genealogy of recent species has been traced back to their common ancestor with enough certainty to illustrate the modes of evolution [19]. Paleontology, lacking a complete fossil record, cannot solve all taxonomic problems; but whenever fossils are present, they offer definitive evidence of an animal's relationships.

Embryology. The embryologic or ontogenetic development of a species may also contribute to the interpretation of its taxonomic position. The immature stages of development in a species frequently reveal relationships which are not discernible in the adult form. The unicelled zygote, or fertilized egg, of vertebrates resembles a remote protozoan ancestor, whose living derivations are now such organisms as the *Amoeba* and *Paramecium*. The gill pouches of embryonic mammals indicate a common origin of all vertebrates. These embryonic gill pouches develop into the respiratory organs of fish, the tympanic cavities of amphibians, and such structures as the Eustachian tube and inner ear of mammals. Figure 2-4 shows that the larva of a urochordate (an immobile form of chordate) is strikingly similar to the adult amphioxus (a cephalochordate), which is the lowest chordate resembling the vertebrates. Adult species of lower organisms resemble many of the developmental stages that a frog passes through. The early developmental stages indicate animals of more remote ancestry than the late stages until the unique form of the adult frog is attained. The zygote is generally comparable to a solitary protozoan, the blastula (a hollow sphere of cells) to a colonial protozoan, the gastrula (a two-layered, cup-shaped embryo) to a hydra, the early tadpole to an am-



(a) Larval urochordate



(b) Cephalochordate

FIG. 2-4. The larval urochordate is strikingly similar to the adult cephalochordate as indicated by the notochord, dorsal nerve cord, and paired gill slits. The adult urochordate loses some of these features which characterize it as a member of the phylum Chordata. [*From H. V. Neal and H. W. Rand, Comparative anatomy. New York: McGraw-Hill–Blakiston,* 1936. *By permission of the publishers.*]

phioxus, the late tadpole to a fish, and the metamorphosing tadpole with legs to a salamander. This ontogenetic recapitulation of phylogeny, sometimes called the "biogenetic law," is not exact because an embryonic frog never becomes a protozoan, hydra, amphioxus, fish, or salamander, although it may resemble these in a general way at different stages in development. The egg is destined to become a frog as soon as it is fertilized. These correspondences, however, do suggest phylogenetic relationships which are often obscured by superficial specialization in the adult structure.

Physiology. The physiological mechanisms of animals often provide additional material for phylogenetic comparisons. Responses to heat and light often indicate differences between groups of animals. Some species become dormant or succumb to temperature extremes sooner than others. Serological studies have been used taxonomically and contribute to the solution of taxonomic problems when morphology offers few clues. For example, the serology of whales indicates they are more closely related to the artiodactyls (even-toed hoofed animals: cow, goat, deer) than to any other terrestrial mammal [3]. This similarity between artiodactyls and whales suggests that whales originated from an ancestor which also diverged into artiodactyls. Certainly such a deduction could not be made on the basis of morphology, since adaptation to aquatic life has necessitated extreme modification. At the specific and subspecific level the genetics of blood groups has proved useful in the analysis of gene frequencies of mammalian populations. These long-term, detailed analyses have provided taxonomic information only in those species which have been carefully examined, such as man, where they have suggested racial affinities and divergences in the absence of cultural artifacts.

Genetics. The course of evolution and consequently phylogeny is determined by the mutability and frequency of genes. All studies of the phenotypes, such as morphology, embryology, and physiology, are based on the assumption that the phenotype is a reasonably accurate representation of the genotype. Any phenotypic character which is exclusively determined by the environment is discarded as a taxonomic criterion. If the size of a snail shell is controlled by the calcium content of the surrounding water, then shell size cannot be used taxonomically. Relationships are established only through inheritance, and the commonality of genetic factors determines the degree of the relationship. Genetics is, therefore, the ultimate tool for ascertaining taxonomic affinities. The decisiveness of genetics, however, is counteracted by the difficulty of doing genetic experiments in a large number of species. Genetic studies will probably be used for taxonomic purposes on only a few recent species; extinct species are forever lost to genetic inquiries. Genetic studies of a few species, however, can provide useful indexes for the analysis of others.

For example, the genetics of the fruit fly *Drosophila* has served as the basis for the interpretation of phylogenetic relationships in other animals.

Zoogeography. The geographical distribution of animals offers many clues to their relationship, since organisms originate in one geographical location. The range of the species may later be extended allowing further divergence to occur both in the center of the original range and at its periphery. Isolation in parts of the original population either by distance or barriers may permit differences among the segments to increase. The taxonomic relation between the original population and the diverging populations may become remote, but their common ancestry can still be discovered by examining the patterns of dispersal and isolation which caused the present distribution. The camel family includes the Bactrian camel of Asia and the llama of South America. Not only are they superficially unlike in appearance, but they also occupy ranges which are separated by oceans. This distribution and morphological divergence is interpreted in the light of paleontological evidence and what is known about the emergence and submergence of the continents. All the camels apparently evolved in North America and dispersed over an Alaskan land bridge to Asia and over the Central American land bridge to South America (Fig. 2-5). As the climate changed and the land bridges submerged under the sea, the camels of North America became extinct and the present-day remnants were isolated in suitable habitats where they

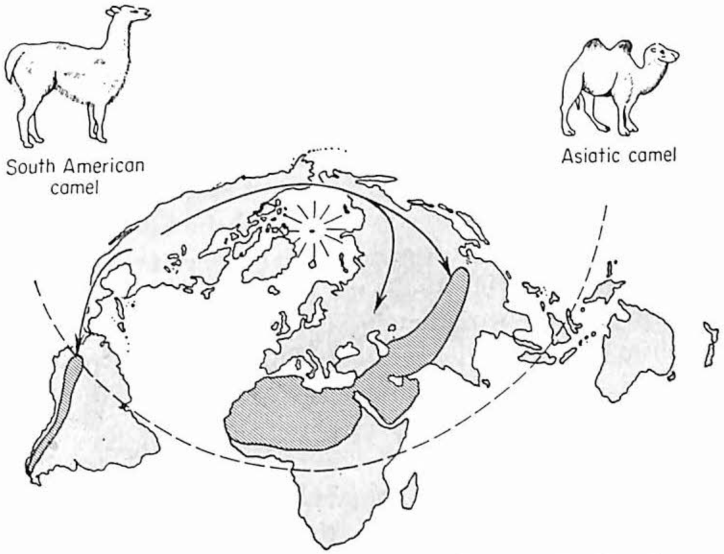


FIG. 2-5. The world-wide distribution of present-day camels. Camels originated in North America and migrated in the direction of the arrows.

differentiated from each other. In lower taxonomic categories, such as species, related species tend to occupy adjacent or nearly adjacent ranges because the isolation period has not been long enough for evolution to proceed to higher generic and familial levels.

Ethology. Ethology is the study of behavior, particularly those patterns of behavior which are predominantly affected by genes. Since zoological taxonomy recognizes only genetically determined characters, it is necessary to distinguish between innate and acquired behavior. Such a distinction may have little value or validity in understanding behavior, as Chapter 3 on innate behavior demonstrates, but it is important in the interpretation of phylogenetic relationships. No behavior, like no anatomical structure, is determined by either heredity or environment acting as discrete and divisible units. Rather, behavior is a product of one interacting within the other through a finite period of time. Awareness of this interaction does not prevent the taxonomist from searching for innate behavior which serves to classify a species of animal. Occasionally behavior is more useful than morphological features for ascertaining an animal's ancestors. A number of such examples illustrate this fact.

The ability to construct the complex orb web by one family of spiders is considered to have arisen only once in the phylogeny of spiders. Consequently, all spiders that construct such a web are placed in this family without regard to their variation in size and geographical distribution [16]. Parallelism in the unique social structure of insects is likewise considered rare and such insects as ants, bees, and termites are often classified on the basis of social structure. Observations of feeding, fighting, mating, resting, and vocalizing behavior may also furnish classificatory data. Recording devices, such as the sound spectrograph, make possible the examination and comparison of the vocalizations of insects, amphibians, and birds [2]. The vocalizations and mating behavior of pigeons have been studied in the laboratory in order to ascertain phylogenetic relationships [22]. Courtship display in ducks is largely inherited, as indicated by the plumage coloration and its employment during the display [5, 11]. Postures exhibited during the display may also reveal species differences. Five distinct postures in the courtship pattern of one species of ducks (Mallard) have been used to form a basis of comparison with other species and genera [5].

From the viewpoint of the zoological taxonomist, behavior is unsuitable as a single taxonomic criterion. However, in species of questionable relationships, behavior may confirm the relationship indicated by other criteria or may suggest alternative affinities. When the behavior of a species points to one relationship and other criteria to another, the relative merits of each criterion must be examined and evaluated. There is no general rule which can be applied to such evaluation for purposes of zoological taxonomy, although all characteristics utilized must ultimately satisfy the principles of evolution.

Review

Modern zoological classification is based upon similarities and differences among animals in an effort to establish their common ancestral relationships, that is, their evolution from one form to several different forms. In order to discover these lines of descent, it is necessary to examine all the available evidence offered by morphology, paleontology, embryology, physiology, genetics, zoogeography, and ethology. The classification of the various animal forms observed today, or once present in the known history of the earth, is based upon the evolutionary processes. Four such processes are described: variation, isolation, selection, and random genetic drift.

Zoological classification offers the comparative psychologist a systematic basis for selecting animals of known relationship for study and has served as a pattern for the classification of behavior. In the next section, "Behavioral Taxonomy," a general evaluation of zoological taxonomy as applied to comparative psychology is first presented. This is followed by a brief description of several classification systems based primarily on the analysis of behavior.

BEHAVIORAL TAXONOMY

Evaluation of Zoological Taxonomy for Comparative Psychology

The original objective of comparative psychology was to trace the evolution of "mind" and "intelligence" in the animal kingdom. This analysis was undertaken by the unqualified adoption of the system used in zoological taxonomy. This adoption was justified by the belief that mind and anatomical structure were related and mind evolved along with structure. Once behavior was "plugged into" the zoological model, it would be possible to trace the evolution of "mind." Since this treatment implied that the anatomy of an animal "caused" or somehow "defined" its behavior, it would be possible to infer the behavior of an animal from its phylogenetic position. Historically, the system of zoological classification did provide stimulating concepts that were used in early research. Furthermore, it provided a rationale for comparative studies.

Two things happened, however, which reduced the value of the zoological system for comparative psychology. First, there was a shift in psychology's object of study from the highly ambiguous concept of mind to the somewhat less ambiguous concept of behavior. With this shift there were developed new analytic procedures which could be applied to behavior. The increase in analytical precision in psychology accompanying this shift made it possible to break down behavior into units which could be dealt with objectively and experimentally. With this change zoological classification became useful only generally in understanding behavior in different animal forms. An example of the broad type of analysis, using the taxonomic model, is given by Nissen [15]. Examination of Figure 2-6 shows that there is a superficial correlation between structure on the one hand and behavior ("intelligence") on the other hand. As we move from the simple (low) to complex (high) structure, we find "intelligence" increasing from low to high. However, this correlation holds only with respect to major animal groups. *When each dimension of behavior is analyzed at the different phylogenetic levels, the relationship tends to break down and certain continuities are lost.*

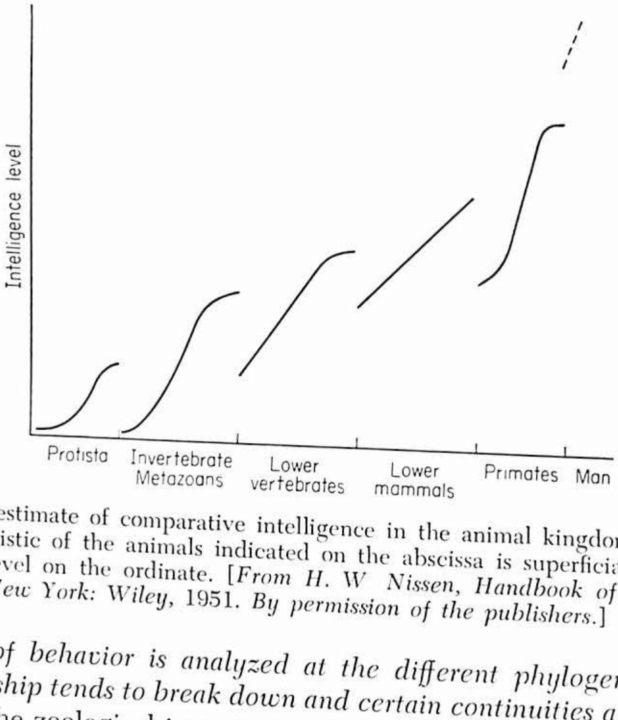


FIG. 2-6. An estimate of comparative intelligence in the animal kingdom. The structure characteristic of the animals indicated on the abscissa is superficially related to intelligence level on the ordinate. [*From H. W. Nissen, Handbook of experimental psychology. New York: Wiley,* 1951. *By permission of the publishers.*]

Second, the zoological taxonomic system is found to be inadequate for comparative psychologists because:

1. The zoological system fails to provide a model which permits accurate prediction of behavior from one phylogenetic level to another [15].

2. It involves inferences based upon extinct forms whose behavior cannot be studied, and the behavior-structure correlations cannot be verified. We cannot study the "history" of behavior as we study the history of an animal form. Behavior is a contemporary event and can only be studied in recent animal forms.

3. In some cases, zoological taxonomic groups are classified on the basis

of structures which do not affect behavior to a great extent. For example, it has been pointed out that the wood rat has been more closely related to the meadow mouse than to the laboratory rat because both possess homologous cheek teeth with rounded cusps in two longitudinal rows which are not shared by the laboratory rat. These lateral cusps are certainly involved in eating behavior, but they play only a minor part in the acquisition, storing, and preference of food.

For these reasons, the zoological system has not completely served the purposes of psychologists. The major use of the system in comparative psychology today is to furnish a systematic basis for specifying the manipulation of the animal as the independent variable, i.e., for selecting animals which are "closely" or "remotely" related. Even this apparent advantage has the associated disadvantage of being primarily a qualitative rather than a quantitative manipulation. When we manipulate the animal variable by choosing two related species, according to zoological classification, the animals may differ structurally in several ways, and it becomes difficult to specify which of the structural differences is to be correlated with a given change in behavior. It can be said with some justification, therefore, that the zoological taxonomic system does not furnish a sound basis for the fruitful organization of the data with which comparative psychology must deal.

Contemporary Method in Comparative Research

The student may well ask, "What is to be done with the data of comparative behavioral studies if the system used in zoological taxonomy is inadequate?" Though behavioral study has no comparable classification system of its own within which its data can be organized, the development of such a system is a major problem confronting comparative psychology.

The beginning of a solution may be found within comparative behavioral study itself—in its aims and methods. Comparative psychology still has as its *aim*, as McBride and Hebb [14] have noted, the determination of "what correlations may exist between structure and function even though they must be imperfect." Kantor [9] cautions that the current approach should begin in behavior and proceed to structure. Nissen [15] gives an idea of how this is to be accomplished and cites the peculiar merit of the comparative method in behavior study. He notes that although within any one species the manifestation of the behavior may be obscured by other processes, when that process is observed in various contexts, the irreducible minimum or essence of the process becomes clear.

In the *contemporary method*, a search begins with the study of behavior and then proceeds to correlate behavior with structure. Behavioral dimensions are arranged to show quantitative variation from simple to complex. At each level the behavioral dimensions are in juxtaposition with the structure characteristic of that level. The attempt is then made to find a common feature in the array of structures which accompanies the variation in behavior. An illustration of this method is presented by the study of Lorenz [11].

Problems in Behavioral Taxonomy

In attempting any classificatory system, the first problem is the definition of the phenomenon to be analyzed, in this case "behavior." At present there is no clear-cut definition of behavior which is acceptable to psychologists and biologists alike. A broad definition should be selected, since the study of behavior is still in its infancy, and both experimental and naturalistic data should be covered. Such a broad definition would be any organismic activity, whether excitation of the retina, a glandular secretion, or muscular reaction. Refinements in the definition may take place as a consequence of the systematization of the data.

Once behavior has been defined, the second problem is to devise a classificatory system of behavior which originates in behavioral data, not in morphological data. This may be done in either of two ways. It may be a *purely descriptive system* where the arrangement of the classes of behavior is made *in vacuo* without reference to the organism. Such a system would not be evolutionary in any sense. The behavioral classes would not be associated with a given organism, though this disadvantage can be offset by applying the descriptive criteria used in the classification to a large number of animal groups. A second system may utilize the analytic mode of the zoological taxonomists. Given a number of animals with varying behavioral characters, or traits, the attempt can be made to describe these as fully as possible in each animal, denoting the unique combinations of characters which distinguish one animal from another. The task is, as Lashley has noted, "to trace out the development of distinct (behavioral) entities as one may trace the evolution of the heart, the gill arches, or the limbs [10, p. 30]."

A third major problem is the selection and specification of analytical units (traits) to be used in the description of behavior. Numerous approaches to this problem have appeared. For example, Warden, Jenkins, and Warner [21] have presented in the following outline a general classification of behavior which is common to all living systems although differing immensely in concrete expression:

Receptive Capacities

Capacity	*Stimulus domain*
Chemoreception	Chemical
Thermoreception	Temperature

Receptive Capacities

Capacity	*Stimulus domain*
Contact reception	Pressure
Phonoreception	Sound
Photoreception	Light
Electric and magnetic reception	Electricity and magnetism
Statoreception	Gravity and inertial stress
Internal reception	Various internal stimuli

Reactive Capacities

- Action system: motor, secretive bioluminescent, and bioelectric mechanisms
- Feeding behavior: activities associated with the securing and ingestion of food, water, etc.
- Protective behavior: autonomy regeneration, avoiding and defense reactions, modes of attack, fighting, etc.
- Reproductive behavior: primary sexual activities, courtship, mating, care of the young, etc.
- Special types of behavior
  - Inactive states: hibernation, sleep, hypnosis, etc.
  - Sound production and communication, etc.
  - Group behavior, intraspecies: aggregation, migration, leadership, domestic and familial relationships, play, etc.
  - Group behavior, interspecies: parasitism, symbiosis, commensalism, biotic community life, etc.
  - Orienting behavior: positive and negative orientation to various sorts of stimuli, homing, etc.
  - Temperament and emotional expression
  - Motivation factors in behavior: incentive-drive indices and the relative importance of these factors in typical life activities
  - Modifiability of behavior: learning-retention indices showing range of capacity to form new patterns of adjustment
  - General intelligence: general level of behavioral capacity based on indices of receptive and reactive capacities

A number of special activity types of more or less limited distribution have been grouped together under “Special Types of Behavior.” The outline represents merely a cross section of behavior of the individual. This general plan of analysis can be used in determining individual, age, sex, and species differences with respect to a given type of activity. The following outline derived from Nissen [15] is also designed to include *all* behavior:

1. Anatomic-physiological foundations
   a. Differentiation of part and specialization of function
   b. Autonomy of parts and regenerative capacity or substitution of parts
   c. Poikilothermic versus homeothermic
   d. Maturation rate

2. Cognitive functions
   - *a.* Sensory discriminations
   - *b.* Perception
   - *c.* Learning
   - *d.* Abstraction, generalization, transfer, transposition
   - *e.* Concepts and symbolic behavior
   - *f.* Language
3. Motivational aspects
   - *a.* Genetic and environmental determinism
   - *b.* Biogenic versus psychogenic motivation
   - *c.* Purpose
   - *d.* Scope of needs
4. General adaptive characteristics
   - *a.* Diversity, richness, and complexity of behavior
   - *b.* Plasticity versus fixity of behavior
   - *c.* Socialization, cooperation, specialization, and division of labor
   - *d.* Cultural accretions
   - *e.* Awareness and consciousness
   - *f.* Behavior aberrations
   - *g.* Importance of individual as opposed to race

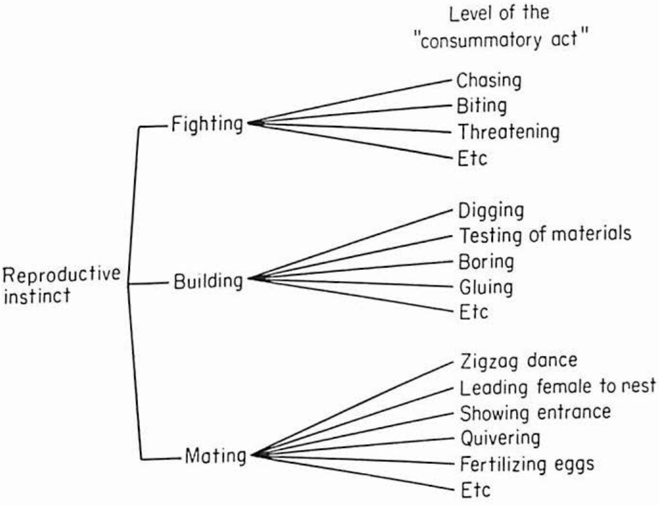
Three Analytic Examples

In contrast, the classificatory systems designed by Lorenz [11] and Tinbergen [20], which are described in the following sections, have dealt with *small* segments of behavior. The former have been concerned with the descriptive, abstract approach to behavior, while the latter have been analytical and concerned with the concrete behavioral events themselves. All have in common the characteristic that they propose terms which are applied to various kinds of behavior and abstractions from behavior. The classificatory value of the respective sets of terms depends upon the clarity of their definition and how extensively they can be applied to behavior.

Three examples of the analytical, concrete type of classificatory scheme are the classifications of Tinbergen [20], Scott [17], and Lorenz [11]. These classifications are concerned with specific "consummatory acts" and deal with limited concrete kinds of behavior in only a few groups of animals which are observed under field conditions.

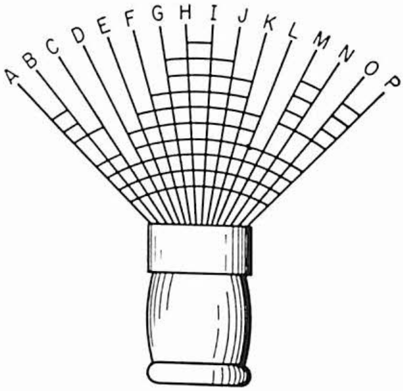
Tinbergen. The elements of Tinbergen's scheme, which deals with the behavior of fish, may be seen in the diagram below.

It can be seen from the diagram that Tinbergen has taken a class of behavior and subdivided it into three smaller elements which, we may assume, are consistently correlated. Each of these subclasses is defined in terms of particular acts. This system may be criticized because some of the acts are ambiguous and depend upon how the observer sees them, e.g., "threatening," "testing of materials," etc. Further, it is questionable whether the subclass of "fighting" is diagnostic of reproductive behavior. Certainly, in other animals, fighting is also associated with dominance-subordination relationships. The scheme, however, appears to be adequate for comparisons of reproductive behavior of fish.



Scott. The system employed by Scott [18] deals with general social behavior, which he has illustrated with a comparison of the behavior of dogs and wolves [17]. This system classifies canine social behavior into the following groups: investigative, allelomimetic (imitative), epimeletic (giving of care and attention), et-epimeletic (attention getting), agonistic (conflict), eliminative, sexual, ingestive, and contactual. In general the above classes are better defined than in Tinbergen's scheme. For example, Scott's terms for defining the sexual behavior of the male dog are running with the female, forepaws extended with the body thrown back on haunches and head to one side, licking female genitalia, mounting, etc. The major merit of the system is that it permits the treatment of a rather broad class of behavior in terms which leave little to the interpretation of the observer. Definitions of classes in such terms permit wider agreement among observers than would be the case in Tinbergen's system. Along with Tinbergen's system, however, Scott's suffers the disadvantage of including certain behavioral patterns which may not be diagnostic of that class, e.g., running with the female may be included either in sexual behavior or in allelomimetic behavior.

Lorenz. Lorenz's system is interesting because it uses minute, concrete aspects of behavior in determining phylogenetic relationships. Lorenz breaks the specific acts in the courtship behavior of ducks into molecular *movement elements*, e.g., head bendings, feather fluffing, and wing spreading. He found these elements were consistently correlated as units in the complex courtship display pattern. When he compared the courtship display patterns of seventeen species of ducks and a hybrid, he observed that they exhibited one or more of these movement elements. His results are presented in the following diagram, which demonstrates the phyletic relationships among the seventeen species [1]:



The relationship of living species may be visualized as the arrangement of bristles in a shaving brush standing vertically. The square at the bottom of the diagram represents the common ancestor. Species in this diagram are shown as lines following the direction of the brush bristles; display elements are represented by a series of arcs crossing these and touching the lines of only those species which exhibit that particular characteristic. The "ancient" display forms, which are common to all the groups studied, are represented by the lower arcs crossing all the bristle or species lines. Toward the top of the diagram, lines joining two or three of the species lines indicate display patterns which are confined to two or three closely related species. As in Scott's system, Lorenz's classes are well defined; however, the definitions in terms of movement elements are too precise to permit extensive application beyond a single genus.

The three systems of classification illustrated above make it possible to establish the following criteria for the specification of behavioral traits:

1. The behavioral traits must be (*a*) concrete aspects of the behavior or (*b*) abstractions based on these concrete aspects of behavior.
2. The traits must be described in terms which make possible high agreement between observers of the same event.
3. The behavioral traits must be consummatory acts, e.g., the final consummatory sexual act (copulation) or complexes of consummatory acts (mating behavior).

4. The traits must be diagnostic of particular behavioral classes and not applicable to more than one class.

In addition, it is necessary to take into account behavioral homologies and analogies. When we study the behavior of a number of animal groups, we often find that certain actions are strikingly similar in two or more animal groups or in two or more individual animals of the same species. For example, two species of fish in the carp family engage in a form of behavior which is similar in both species. The males come to rest parallel to each other in the water and then rhythmically extend all the fins to the fullest. This is sometimes called "threatening" behavior. The question arises whether these behavioral patterns in both species are alike because they have been acquired independently with a similar superficial function (analogous) or because the fish have the same common ancestor (homologous). This problem has been directly faced by Lorenz in the classification system presented above, though it has not been answered for many other types of behavior which occur among related species.

With the above criteria for the specification of behavioral traits, it may be possible in the future to construct a scientific classification of behavior parallel to, but not identical with, that of zoological taxonomy. Such analysis of behavioral traits provides an inductive approach, from which correlated traits may serve to form broader classes of behavior and ultimately arrive at generalizations and hypotheses suitable for experimental testing.

SUMMARY

The process of a scientific classification is the selection and definition of traits, the correlation of several traits, and the organization of the traits into classes which are exhaustive, unitary, and mutually exclusive. A scientific classification provides order in the natural universe, definitions for analysis, relationships of complex phenomena, and hypotheses suitable for testing.

These principles are utilized in zoological taxonomy, which is based upon the phylogenetic relationships in the animal kingdom. Phylogenetic relationships are established by the evolution of several different species from a common ancestral species. Evolution occurs where there is variation, isolation, selection, and/or genetic drift. Phylogeny can be interpreted only from homologous traits, although animals sometimes resemble each other because of convergence or parallelism. Zoological taxonomists use criteria from morphology, paleontology, embryology, physiology, genetics, zoogeography, and ethology to establish evolutionary lines of descent.

Contemporary methods of classifying behavior *begin* with the study of behavioral processes and then proceed to correlate them with structure. This method was illustrated by three systems of classification of behavior, and the criteria for the specification of behavioral traits were derived from these systems.

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CHAPTER 3

Innate Behavior: The Organism in Its Environment

INTRODUCTION

Definition of Instinctive Behavior

The term "instinct" has two distinct meanings which must be kept separate for adequate communication, but which are often confused or used interchangeably. One meaning, which is of limited scientific value, is explanatory. The term is used to explain *why* certain behavioral patterns occur. For example, if an organism is very aggressive, this behavior can be interpreted as being caused by an instinct of pugnacity. Another example is the common statement that birds fly to a warmer climate when winter approaches because they have an instinct which warns them of the coming cold. When used in this manner, the term "instinct" often leads to a scientific dead end because the behavior has now been "explained" and there is no need to investigate further.

The second usage of instinct is that of describing certain behavioral patterns with no connotation of explanation implied. Here, the term refers to relatively complex, unlearned, innate patterns of behavior. In this sense, instinctive behavior stands at the top of the list of unlearned behaviors, which also includes reflexes (relatively simple movements of parts of an organism) and tropisms (reflex actions of the entire organism). A list of some of the behavioral patterns which have been classified as instinctive has been given by Lashley [21]. Among these behaviors are homing of pigeons, migration of fish, mating behavior of the female rat in heat, web weaving of spiders, reactions of the sea gull to artificial and normal eggs, nest building by rat at her first litter (primiparous), cleaning and retrieving of young by the primiparous rat, and visual reactions of rats reared in darkness.

When used in the descriptive sense, the term has some taxonomic value for categorizing behavior (see Chap. 2). In addition, by not implying an explanation of the behavior, the way remains open for further research aimed at isolating the mechanisms underlying the behavioral pattern. Later in the chapter examples will be given of this type of research with reference to maternal behavior of the primiparous rat. On the other hand, implicit in the second definition is the classification of behavior into learned and unlearned categories. We shall have more to say about this dichotomy later on. The reader should keep both definitions in mind while reading this chapter.

Historical Background

The concept of instinct has been traced back at least 2,500 years in the ancient Greek literature [5]. It has survived over the years, perhaps, because it is generally considered in relation to the broad and philosophical problems of human behavior: the differences between animals and humans, the place of man among the organisms, the relation of reason to human behavior. In the Middle Ages a clear separation of man from other animals was made. The behavior of animals could be understood and explained in terms of their brutish instincts, while man possessed the power of reason and divine properties.

Darwin found it necessary to eliminate this dichotomy and introduce a major continuity hypothesis relating man and animal. In Darwin's approach it was essential to establish the evolution of mental as well as structural properties of organisms. On the other hand, it was important to show the role of instincts in human behavior in order to establish the continuity of man with the other animals. The Darwinian concept of instincts in human behavior was accepted by such early psychologists as Spencer and William James. Beach [5] has pointed out the influence of this concept upon McDougall's list of human instincts and the role accepted for instinctive drives and needs by Woodworth and Thorndike. The concept of instinctive behavior was accepted as a basic principle by psychologists around the beginning of this century.

Objections to Instinct. One major social psychologist, Asch [2], has discussed Darwin's contribution in relation to its impact upon psychologists primarily interested in human behavior. His evaluation is that the doctrine of evolution was used by psychologists to "dehumanize" man. The special characteristics of man (e.g., his particular capacities for social life, his potentialities for science and art) were not considered to be unique contributions of the human species which enriched the realm of biological phenomena. Instead, these characteristics were reduced to the model of action in lower organisms. Asch pointed out that one of the consequences of Darwinian thought was to place man in nature, yet take away from him the qualities most distinctive of humanity—social relations, speech, and art. He feels that this dehumanization of man has dominated much of current thought and that psychology has not yet recovered from this approach. "A considerable effort was directed to forming a psychology based predominantly on the study of lower organisms, the principles of which were generalized to the human level. This shift was marked by a radical omission or devaluation of specifically human characteristics . . ." [2, pp. 9 to 11].

Not only have psychologists interested in human behavior from an evolutionary point of view been concerned with the problem of instincts, but animal and comparative psychologists have considered this as well. Through the 1920s and 1930s a major argument raged over the problem of instinct. Beach refers to this as "the anti-instinct revolt" and characterizes it as a "war over instinct . . . fought more with words and inferential reasoning than with behavioral evidence" [5, p. 404]. Part of the rebellion was brought about by the inordinate number of behaviors classified as instinctive. It soon became apparent that the number of instincts postulated was almost as great as the number of behaviors observed. Lashley [21], in discussing the anti-instinct movement, pointed out that this rebellion was also against the postulation of imaginary forces utilized as explanatory concepts to interpret behavior. The rebellion carried in its path not only the notion of instinct but also the mechanism by which these instincts were presumed to be transmitted, namely genetics. Thus, in discarding instinct theories, psychologists also appeared to lose interest in the study of genetic determinants of behavior.

Renewed Interest in Instincts

In his discussion of the anti-instinct movement, Beach shows that the revolt failed because those who led it were forced to assume a two-factor theory of behavior: that any behavior is innately determined and reflexive in nature or else entirely learned. This dichotomy of reflex or learning could not stand up under careful examination. The notion of instincts, defined by Beach as "complex, unlearned patterns of behavior" [5, p. 405], was readmitted into the scientific vocabulary.

However, the question of innateness of behavior, though scientifically acceptable with the readmission of instincts, did not occupy a central position in the research efforts of psychologists. Over the past twenty-five years the major research emphasis in this country has been upon learning and motivation. Most of this research has been performed on less than a half-dozen species, and few attempts have been made to obtain interspecies comparisons, which may be indicative of genetic differences, or even intraspecies comparisons of animals with different genetic histories [36]. This lack of intraspecies comparisons is true even for the large amount of research on the rat, as a cursory examination of Munn's *Handbook* [30] will show. In recent years there has been again an upsurge of interest in the study of instincts stemming primarily from the works of

Lorenz [26] and Tinbergen [43], who are prime workers in a biological discipline dealing with animal behavior, i.e., *ethology* (see Chap. 1). The findings and theoretical interpretations of these researchers have influenced American psychologists to reinvestigate the problem of innate determinants of behavior.

The next section presents a logical and experimental approach to the problems of the innateness of behavior, including such concepts as instinct and maturation, through the study of the development of behavior. Following this, there are sections on research findings and theoretical interpretations concerning instinctive and maturational behaviors which have been investigated by psychologists and ethologists.

THE DEVELOPMENT OF BEHAVIOR: THE ORGANISM IN ITS ENVIRONMENT

In the previous section we summarized some of the earlier concepts concerning instinctive behavior. Three major parameters, or factors, may be recognized. These three parameters are concerned with heredity, environment, and time. Instinctive behaviors, since they are by definition unlearned, must be rooted in the *hereditary* make-up of the organism. This is also true of those behavioral patterns which develop through a maturational process, except that they occur later in *time*. Both of these patterns are, by definition, free of learning, practice, or other specific effects of the *environment*. These are the three fundamental parameters manipulated by any scientist who works with living matter. The research of any worker, whether he is studying a microorganism implanted in a culture, the activity of an organ in vitro, or the complex behavior of a primate introduced to a strange social situation, can be classified along these three dimensions. Though these dimensions have been discussed in other chapters, it will be convenient to present a brief discussion of them here for purposes of presenting afterwards a synthesis of these parameters.

Heredity

By heredity is meant the characteristics and the effects of the genes (including interactions among genes) present in the fertilized egg at the moment of conception. Since it is difficult at our present stage of technology and knowledge to study the genetic constitution of the fertilized egg directly, the analysis of hereditary characteristics has to be approached indirectly. This can be done by studying the extremes of a population [24, 27], comparing different species on equivalent tasks, using purebred strains [37], or partially inbred strains [35, 38].

In studying the extremes of a population the approach is to take a characteristic in which we are interested (e.g., coat color, intelligence), obtain organisms which can be classified into two groups on this characteristic (presence or absence, greater or lesser amount), and breed these organisms following standard genetic procedures.

Since different species have different hereditary backgrounds, obtained differences in performance on equivalent tasks reflect genetic differences. This is, of course, the area of the comparative study of organisms (e.g., comparative anatomy, comparative physiology, comparative psychology). One example of this approach is the study of methods of locomotion in different organisms in which the differences obviously reflect genetic differences. On another level, there is the comparative study of intelligence of different species by means of delayed-reaction measures, discrimination learning, problem boxes, etc.

A third approach to the analysis of genetic factors is to develop a number of highly inbred strains of the same species. A strain is purebred when all animals within the strain can be expected to have 99 per cent or better of their genes in common. Working *within* any one strain permits the type of genetic analysis described under the first method. Since there are a large number of different strains, reflecting different genetic backgrounds, differences *among* strains indicate differences due to heredity as described in the second method. An example of this approach is the genetic analysis of audiogenic seizures. Other examples are given in Chapter 11.

A fourth approach to the study of heredity, which is really an approximation to the previously described method, is the use of partially inbred strains. This differs from a purebred strain in that a lesser percentage of genes is common among different organisms from the same strain. Since it takes from twenty to thirty generations to approach pure homogeneity, which may involve a number of years of breeding, research can be conducted at the same time that the breeding program is going on. Although the use of partially inbred animals is a helpful technique, there are complexities because of the heterozygosity present among these animals. Ross, Ginsburg, and Denenberg [35] have discussed the advantages and disadvantages of the use of partially inbred strains in psychological research.

Environment

Broadly speaking, any factor internal or external to the organism which affects that organism may be considered an environmental factor, exclusive of gene characteristics and their effects.

Research on environmental manipulation has, in general, been the special province of the psychologist, as hereditary manipulation has been the special research field of the geneticist. In general, psychologists have not been concerned with rigid definitions of environment. They have usually worked with organisms at some point after conception and have deliberately manipulated environmental factors at these points in time. Their definitions, thus, have been in terms of experimental operations.

Psychologists, in their research on environmental influences upon behavior, have generally avoided manipulation of hereditary variables. They have, in fact, developed methodologies whereby genetic factors will be balanced out. One such technique is the use of large numbers of subjects, so that individual differences in genetic characteristics will be equated. Another method is the use of the split-litter technique [30] in which subjects from the same litter are randomly assigned to a control group and one or more experimental groups. This method is of limited usefulness when partially inbred strains of animals are used and can even be detrimental to the objectives of the experiment [35].

Under this broad category of environment can be subsumed most of psychological research. These investigations will be discussed, to some extent, in several of the other chapters. They include learning, motivation, sensory processes, problem solving, perception, intelligence, abnormal behavior, social behavior, etc. All of these events are studied by introducing some modification or modifications of the "conventional" environment and noting how behavior changes. Often, although not always, control groups not receiving the environmental modification are utilized as a base line for comparison with the experimental group (the group which has had the environment modified). If behavior changes as a function of the experimental manipulation, conclusions are drawn concerning the effects of the modification.

Time

This is the dimension which is correlated with maturational and other developmental changes in the organism. It is usually measured in one of the convenient physical metric systems such as seconds, minutes, days, weeks, months, or years. Another measuring scale of importance here is a behavioral time scale associated with events occurring to the organism yet relatively independent of the particular metric times of occurrence. An example is the study by Ross, Denenberg, Sawin, and Meyer [34] of nest building in rabbits. It was found that multiparous females improved the quality of the nests built from the first through the fourth litter which they bore. A further study [13] determined that the quality of nest was not correlated with the particular age of the doe. Here, then, is a situation where a behavioral event—having a litter—is the basic metric, and increases in this scale (having additional litters) are related to the behavioral event of improved nest quality. This latter event is independent of the physical metric scale of age of the organism. Developmentally, we can list a number of critical phenomenological time points for the mammalian group. These are conception, birth, weaning, puberty, maturity, parturition (for the female), senescence, and death.

Another point is that time, per se, is often a psychologically meaningless dimension. The important factor is *what* takes place over time. When changes in behavior over time can be related to other variables (e.g., bearing a litter, the onset of sexual hormones) which can be given psychological or physiological meaning, then a meaningful relationship may be established. Even here the relationship is not fully meaningful until the mechanisms underlying the behavioral changes with time have been worked out.

The Organism in Its Environment

As mentioned earlier, these are the three dimensions which are studied or held constant by any research worker who investigates living matter. The geneticist is primarily interested in the analysis of hereditary characteristics and attacks his problems by maintaining a relatively constant environment for the organisms he is studying. The mouse geneticist, for example, keeps his breeding stock on a standard diet throughout their lives, houses them under essentially the same type of living conditions, maintains relatively constant temperature of the living quarters, etc. The offspring of animals reared in this manner are themselves reared in the same manner. Genetic characteristics of these animals are studied and certain conclusions drawn concerning hereditary mechanisms. The animals may be studied over a time span, although, if so, it is in general relatively short. This is because the geneticist knows that the trait he is studying will usually not vary over time, once it has manifested itself. There are exceptions to this, for example, in the study of constitutional diseases.

While the geneticist maintains a constant environment, works within a relatively narrow time span, and varies the genetic make-up of his organisms, the psychologist generally manipulates the environment while working within a narrow time range and with organisms which are partially inbred or with very large numbers of organisms in an attempt to eliminate the possibility of genetic differences influencing his results. For this type of work the domesticated albino rat, usually within the age range of 80 to 120 days, has been the most important research tool of the psychologist [30].

Other students of behavior have been most interested in the time dimension, or developmental aspects, of the organism. They try to eliminate genetic differences by use of large numbers or of partially inbred strains, and they work within a relatively narrow spectrum of environmental influences. Studies here include Gesell and Ilg's work on developmental schedules in the child [15], Scott and Marston's study of development in the dog [39], Williams and Scott's analysis of mouse development [47], and Small's report on development of the rat [40].

Research workers studying living organisms may be differentiated by the relative emphasis which they place upon the three dimensions of heredity, environment, and temporal sequence in their studies. Each approach can, by itself, give only a limited description of the organism it is studying. Investigators generally work across part of one spectrum while holding the other dimensions constant.

It is because different disciplines emphasize certain dimensions while eliminating others through appropriate experimental methodology and because of the relative isolation of one discipline from another that certain concepts have developed which, when examined critically, are scientifically limited. In particular we are concerned with such notions as learned-unlearned, heredity-envoronment, instinct, and maturation, when they are used as interpretive concepts for behavior.

We suggest that *no* behavior of a living organism can meaningfully be described in terms of only one dimension (it is all learned, it develops with time, it is purely instinctive) but must, instead, be related to all three of the dimensions discussed. We have attempted to present a model of this approach in graphic form in Figure 3-1, where the three dimensions of heredity, environment, and time are integrated. In terms of a descriptive formula, the same concept is described by $B = f(HET)$, or behavior of any living organism is a function of its heredity, the environmental factors present when testing, and its previous life history (time).

The various points along the H and E dimensions are not to be interpreted as reflecting quantitative differences only. For example, the levels of H can indicate different species (e.g., part of the phylogenetic scale) or organisms within the same species which differ in heredity (purebred mice, for example, or partially inbred rats). These, as indicated earlier, are probably the most common methods that psychologists have for the study of genetic variables.

The E dimension can be either quantitative or qualitative. If a researcher presents a graded series of stimulus intensities to an organism (e.g., in determining sensory thresholds), then the levels of E are quantitative in nature. On the other hand, if he compares the relative efficacy of hunger versus thirst as motivators of behavior, this is an investigation of qualitative factors.

The time dimension is, of course, quantitative. The selection of the proper metric scale to use, physical or behavioral, is determined by the researcher as a function of the kinds of variables he is studying and the questions which he seeks to answer.

By examining the three shaded-in blocks within the cube, we can see the general lines of attack of the geneticist, the psychologist, and the student of development. The geneticist works within relatively narrow environmental and temporal spectra and studies variations along the *H* dimension. The psychologist, on the other hand, is interested in varying *E* while *H* and *T* are relatively constant. The researcher studying development holds *E* and *H* constant while observing variations along the time continuum. We can now return to our discussion of instinct and maturation to see how these concepts fit into the model presented in Figure 3-1.

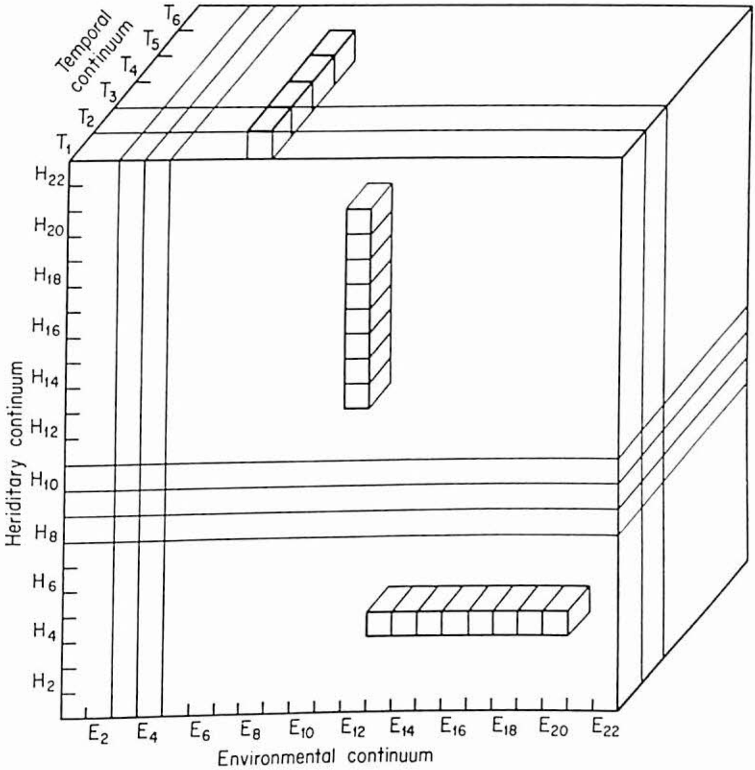

FIG. 3-1. Schematic presentation of the three dimensions of heredity, environment, and temporal sequence. These are the continua with which all researchers working with living matter are concerned. The *H* continuum represents different species or organisms within the same species which differ in genetic constitution. The temporal continuum can be expressed in terms of physical measurement units, such as years, months, or days, or in terms of behavioral events, such as conception, birth, weaning, puberty, maturity, parturition, and senescence. The *E* dimension concerns experiential phenomena generally studied by the psychologist. See the text for discussion of the shaded areas.

Underlying any theory of instinct is the basic assumption of invariability of behavior. This does not mean that the behavior must be identical under similar or dissimilar environmental conditions, but that the behavior will occur and will be readily recognized as being instinctive. Fundamentally, this means that the behavior is innately determined and is independent of specific environmental influences. Sometimes this behavior is manifested as soon as the organism is capable of direct activity (e.g., pecking of birds). Other behaviors do not occur until relatively late in the life of the organism (e.g., nest building). Though both of these activities are classified as instinctive, the behaviors which occur later on and which are dependent upon some prior event, such as neurological development or presence of sexual hormones, are commonly called maturational. These maturational activities are also presumed to be independent of specific environmental influences.

If we select any level of *H* in Figure 3-1 (i.e., any species or genetic strain within a species) and consider any instinctive behavior, *that behavior must occur in the same general form at each and every level of* E *to be properly classified as being instinctive.* The behavior should also be present at all points along the *T* continuum from some point relatively shortly after birth until senescence. *If the behavior first occurs late in time, but is still present in the same general form at all points along* E, *then it is called maturational.* In other words, the only difference between a behavior which is classified as instinctive and one which is called maturational is merely the time of first occurrence of the event. Both of these are presumed to be determined by the heredity of the organism.

All that we have done above is to place or fit the commonly accepted definitions of maturation and instinct into the schema of Figure 3-1. If the behaviors do occur at all points along *E*, then they are independent of *E*, as required by the definitions. However, this relationship must be determined by experimentation and cannot be taken for granted. Nor can we observe behavior at one point on the *E* continuum and generalize on the complete spectrum of environmental events.

Learning or experience is represented along *E* and across *T* as well. It is necessary to determine whether the particular environment in which the organism has been reared has influenced its "instinctive" behavior. In other words, until these presumed innate behaviors are studied with organisms reared under many different environmental conditions so that we have at least an adequate sample of *E*, we cannot logically conclude that the behavior is independent of *E*. It should be noted that the term "learning" is used here in its broadest sense to indicate any unique experience acquired by the animal as a function of exposure to a particular environment.

We can see, then, that to ask whether a given behavior is inherited is an unanswerable question. We must always stipulate the environmental conditions which have occurred throughout the lifetime of the organism (combinations of both *E* and *T*) and state that under these conditions with a particular species, strain, or genetic constitution this behavior is found to occur consistently. Likewise to inquire concerning the percentage of behavior caused by environmental factors and the percentage brought about by genetic characteristics cannot be answered as such. We must again specify the hereditary background, environmental conditions, and temporal sequence in order to answer the question.

We can, of course, design an experiment in which "components of variance" associated with environment, heredity, and time can be obtained. This would be a three-dimensional factorial analysis of variance design with at least two levels of *H*, *E*, and *T*. Variance components associated with each of the main variables can be obtained, and their numerical values compared to determine the contribution of each. Even here, however, we are dealing with fixed factors and cannot make generalizations beyond the particular levels studied. A further discussion of this approach is beyond the scope of this chapter.

In the next two sections we shall consider current theories and research on instinct and maturation. The schema shown in Figure 3-1 will be useful in interpreting the concepts and findings.

THEORIES OF INSTINCT

Lashley [21] has discussed the experimental analysis of instinctive behavior. As an example, he described the maternal behavior of the primiparous female rat. Although reared in isolation, the female will mate as effectively as will females reared in a group situation. She will gather paper or other material and construct a crude nest. When the young are born, the mother will eat the placental membrane, vigorously clean the young, and effectively retrieve them if they wander out of the nest. Lashley states that these behaviors are relatively precise reactions to specific stimuli (both internal and external). These behaviors suggest a number of problems which need to be investigated. These include determination of the nature of the stimuli which elicit the different responses, investigation of the pattern of motor activity by which a given behavior is achieved and, ultimately, specification of the neurophysiology of the behavior. These problems are not unique to this one example but are common to all instinctive behaviors. Within the context of Figure 3-1, this means investigating different aspects of the *E* continuum while holding *H* and *T* relatively constant.

Lashley distinguished between reflexive behavior and instinctive behavior on the basis of the stimuli required to elicit the reactions. The stimuli for reflex behavior are relatively local, while those for instinctive behavior are more general and complex. He states that the term "instinct" should be retained, since it stresses the importance of the problem of sensory organization.

The essential first step in an understanding of instinctive behavior, Lashley felt, was to determine the properties of the stimulus situation which are effective in arousing the instinctive behavior, that is, to *define* the stimulus complex. The difficulty of this task can be seen by considering some research findings on reproductive behavior of the rat. For example, elimination of any one sense modality will not interfere with mating behavior or retrieving of young, though the destruction of two or more senses may reduce or eliminate both of these patterns. Lashley also reported that wide variation in any property of the stimulus is possible without destroying its effectiveness in arousing a response. These data suggest that the instinctive behavior associated with reproduction in the rat is dependent upon a complex of stimuli, some reactions being elicited only by the total integrated pattern, while others may be aroused by single elements of the stimulus.

In considering the mechanisms which underlie reproductive behavior, Lashley concluded that there must be hormonal factors which act upon the central nervous system. Three hypotheses concerning hormonal effects upon the nervous system were considered and rejected: the hormones stimulate the growth or formation of nervous connections; the hormones act merely by increasing the general excitability of the organism; and the hormones bring about physiological changes in the organism. The fourth and most plausible hypothesis is that the hormones act upon the central nervous system to increase the excitability of the sensorimotor mechanism specifically involved in the instinctive activity. Lashley indicated that judgment about the validity of this latter hypothesis should be reserved until more work has been performed.

A recent symposium called together scientists representing the fields of zoology, psychology, and sociology to consider and reexamine the concept of instinct with the objective of common agreement on the meaning of the term [1]. Allee, the zoologist, stated that all behavior could be classified into the two categories of learned or unlearned. There are five levels of unlearned behavior: poorly organized responses of animals lacking nervous systems; reflex arc reactions; kineses (speeding or slowing of unoriented whole-organism responses); oriented tropisms and tactile responses; and instincts, "the most complex of all phases of unlearned behavior."

In his analysis of behavior, Allee pointed out that any act is a function of a constant invariable element interacting with a variable component. These may be grossly classified as genetic and environmental elements respectively. In instinctive behavior the constant element is greater than the variable one, while in intellectual behavior the converse is true. In all cases both of these elements are present though in varying degrees. From this viewpoint any behavior can be theoretically analyzed into two dimensions: genetic and environmental. The classification of instinctive or intellectual will be determined by the relative contributions of these elements. With reference to our conceptual model, Allee is emphasizing the relative contributions of constant levels of *H* and *E* at a particular time *T* upon behavior. That is, given a particular genetic make-up interacting in a specific environment at a point in time, the objective is to determine the relative influence of heredity and environment in determining the observed behavior.

As an example of an instinctive act with a variable element, Allee describes his observations of the behavior of a solitary wasp which he chanced upon one day. The wasp had just stung a caterpillar into immobility and was dragging it back to its burrow where it would lay its eggs on the skin of the caterpillar. The larvae, when they hatched, would obtain their nourishment from the insect. The wasp, disturbed by the intrusion of the human, dropped the caterpillar and then flew around trying to find it. It was unable to do so immediately and began a systematic search of the area (variable behavior). After a few minutes, the wasp had still not located its prey, and Allee picked the caterpillar up and placed it near the wasp, which carried the insect to the burrow, laid its eggs, and then covered up the hole so that it was completely hidden except for a slight difference in color, due to dampness, from the rest of the earth. Rather than flying away, which is the normal behavior of the wasp, the creature hovered around the burrow, apparently disturbed by some aspect of the environment. It then picked up some pine needles lying nearby, placed them skillfully upon the damp spot so that the burrow was completely camouflaged (another example of variable behavior) and then flew away.

Nissen, the psychologist, pointed out that the term "instinct" had been used both as a description of a particular behavioral pattern and also as a motivating agent bringing about behavior (e.g., the instinct pugnacity). He stated that the term is useful only in the former sense. In differentiating among instincts and other forms of behavior, he listed several criteria. These include a relatively long duration in time (as compared to a reflex or automatized habit), elicitation by a complex pattern of both internal and external stimuli which may vary considerably in detail, and considerable flexibility in the manner by which the final result (e.g., bird's nest, spider's web) is achieved. If the behavior is determined by obviously innately determined components, it is commonly spoken of as being instinctive. In comparing instinct and learning, Nissen concludes that these are not mutually exclusive categories. Instead, they are intimately related. For example it is pointed out that "the foraging insect must learn and remember, on the basis of a single flight, the direction or the landmarks which guide it back home . . . the digger wasp even remembers from day to day how well each of its eight or ten burrows is stocked with provisions" [1, p. 292].

Nissen argues that the classification of behavior into different groups (e.g., random, instinctive, habit) requires knowledge of the past history of the organism, and that this demands experimental analysis. He goes on to discuss the relationships among reflexes, instincts, and learning and suggests that these three behaviors can be ordered along the same continuum, which he calls inheritance of "*a more or less specific readiness to learn*" [1, p. 292]. Thus, behavior which we call learning is distinguished from instinctive behavior in that what is inherited is a non-specific readiness to learn, while the highest degree of specificity of learning is seen in reflexive behavior. To test this idea, the experimental procedure indicated in Figure 3-1 would be used. Given a particular organism (level of H) placed in a number of different environmental situations, if the organism could learn only a particular specific response, this behavior would be classified as instinctive. On the other hand, if the response acquired were partially determined by the environment (were non-specific), it would be called learned behavior.

The sociologist Nimkoff discussed the difficult problem of attempting to determine what behaviors on the human level could be considered instinctive. He argued that, when large masses of human beings are studied, individual differences due to genetic factors are balanced out and that behavioral patterns which are common to all cultures *may* be instinctive. That is, if a particular behavior is common to many different cultural settings (levels of E) which are presumed to be similar genetically, since large masses of people are studied, then this may be construed as evidence that the behavior has a genetic basis. One example of this is the family, which is found, in some form, among all cultures. "We conclude that the presence and broad outlines of this institution (the family) are determined by man's biology, but not the details of structure and function" [1, p. 296]. A second example cited by Nimkoff is polygamy in humans which appears more frequently than polyandry. This finding is supported by studies of the primates. It is also pointed out that some universal practices are not biologically determined (e.g., the taboo against incest) and some instinctive acts such as sexual activity may be modified by the culture so that it is not universally present. In concluding his discussion Nimkoff stated, "In short, there does not seem to be any easy formula which we can use for determining what is learned and what is genetically motivated in human behavior" [1, p. 297].

The most recent and thorough experimental program and theorizing on the problem of instincts has been done by the ethologists Lorenz [26] and Tinbergen [43]. One major experimental approach is through the use of dummy models. By use of these dummies, various stimulus characteristics which are effective in arousing the instinctive behavior may be determined. Through this approach, a considerable range of animals and behaviors has been investigated. It is to the credit of the ethologists that they have aroused widespread interest in the basic theoretical problems involved and have developed challenging experimental studies. We shall first present some examples of instinctive behaviors studied by Lorenz and Tinbergen and then present their theoretical analysis.

The graylag goose will retrieve, in a rather stereotyped manner, an egg which has rolled out of its nest. The goose extends its head toward the egg, stands up, and slowly moves forward to stand on the rim of the nest, all the time keeping its head and neck pointed toward the egg and its eyes fixated upon it. The bird then extends its neck so that the egg rests against the underside of the bill. It then proceeds to roll the egg back into the nest by shoving it back between its legs, using the underside of its bill. At times the egg rolls away from the goose by slipping sideways, but this does not always terminate the behavior. The bird will continue its egg-rolling movements until the bill has passed between its legs. By the use of dummy eggs, it has been determined that the necessary characteristic of the stimulus is a rounded contour. Shape and size do not influence the bird if the appropriate contour is present. The goose will roll a cylinder and will also roll an egg which is much larger than the normal goose egg. In the later case the stereotyped nature of the response was obvious, since the goose could not adapt its movements to the abnormal size of the egg that got stuck when pressed between the breast and bill.

The flight and alarm reactions of birds to flying predators have also been investigated. It had been noted that the flight reaction was often elicited by quite harmless birds, even though the shape of the harmless birds was quite different from the predatory birds. However, one factor common to both the predators and the harmless birds was that they all had short necks. It was hypothesized that the special shape of the neck was the adequate stimulus to elicit this behavior. This hypothesis was tested by constructing short-necked and long-necked cardboard dummies. In addition, other aspects of the stimulus, such as shape and size of wings and tails, were also varied. These dummies were pulled by a series of wires over the heads of the experimental animals (ducks and geese). It was found that as long as the model had a short neck the birds would show alarm. Variations of the other characteristics had essentially no effect. To verify the findings about the stimulus value of short necks, the movement of some of the dummies was reversed. These were dummies with short necks and long tails so that when they were turned around, they then had long necks and short tails. In the former instance (short neck) the alarm-escape reaction was elicited, but this did not occur when the long neck appeared first.

Aggressive and reproductive behavior of the three-spined stickleback fish has been intensively investigated. The fighting response of the male generally occurs near the boundaries of its territory when it encounters another male. By the use of dummy fish which varied in different stimulus characteristics, it was determined that the red belly of the male was a stimulus which would evoke fighting. Further research determined that the posture adopted by the stickleback was important. This was determined by putting a stickleback into a test tube so that it could not move. When this model was presented horizontally (normal swimming position), it did not cause fighting, but when the model was turned vertically so that the fish was facing head-down, then fighting ensued. Thus, the fighting response of this fish is dependent upon a combination of the red belly plus the threat posture of head-downward.

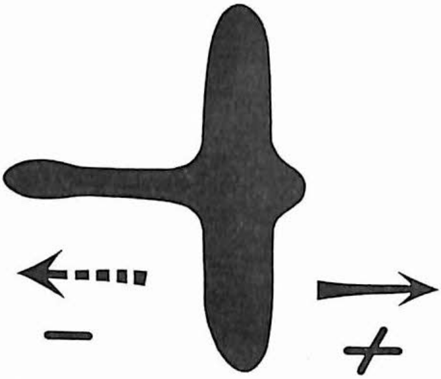

FIG. 3-2. Model of a bird of prey. When sailed to the left (long-necked model), no escape reactions by ducks and geese were noted. When sailed to the right (short-necked model), escape reactions were observed. [*From N. Tinbergen, The study of instinct, New York: Dial Press, p. 78.*]

The courtship behavior of the male stickleback before a pregnant female has been studied in the same manner, and here also it has been found that the behavior is dependent upon two stimuli. One stimulus characteristic is the swollen abdomen of the female. The male will court a crude dummy of a female which has a swollen belly but will generally ignore an exact replica which does not have the swollen abdomen. If the dummy is placed in a particular posture, i.e., facing head-upward at approximately a 45-degree angle, it will elicit courting behavior more often than when placed in other positions.

From their experimental findings, Lorenz and Tinbergen have constructed an elaborate and controversial theory of instinctive behavior. They assume, first of all, a response hierarchy of instinctive behavior ranging from general behavior (e.g., migration of fish to shallow water) to specific consummatory acts (e.g., fertilization of eggs). This behavioral hierarchy is under the control of a hierarchy of neural centers which act as energy systems. These centers are innately determined and function to coordinate all the movements of the instinctive act. Stimulation which triggers off a neural center will set in motion the instinctive behavior. A problem arises here, since the organism is continually being stimulated yet does not continually engage in all of its instinctive behaviors. This difficulty is handled by postulating an inhibiting or blocking center (called the *innate releasing mechanism* by Tinbergen) for each neural center. These inhibitory centers act to stop stimulation from reaching the neural centers which control the instinctive acts and thus prevent their occurrence.

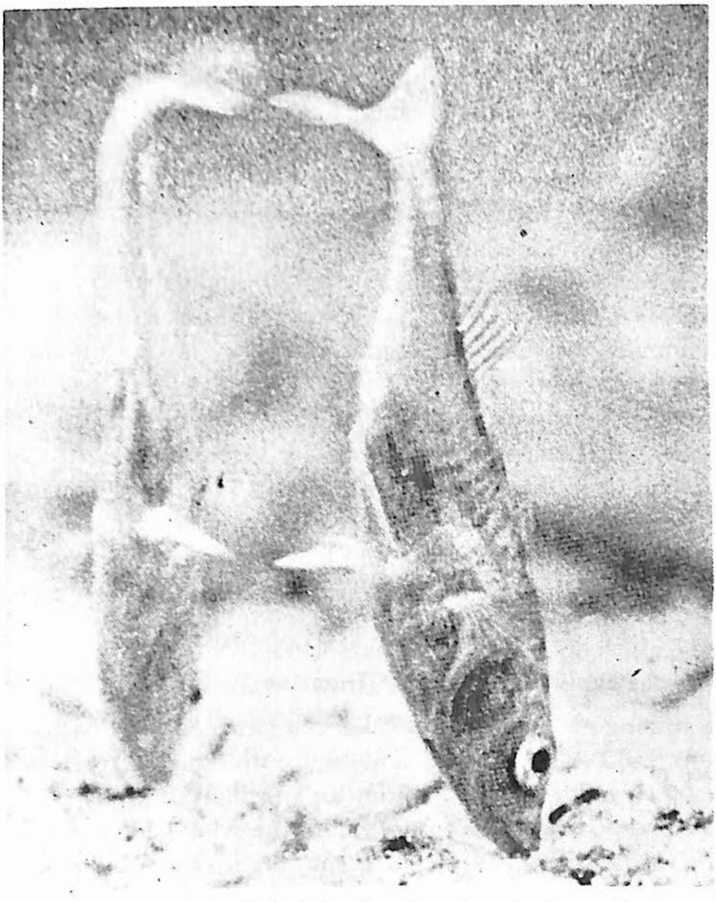

FIG. 3-3. Male three-spined stickleback in threat posture in front of mirror. [*From N. Tinbergen, The study of instinct. New York: Dial Press.*]

The inhibition set up by the innate releasing mechanism is "released" when the appropriate stimulus or stimuli impinge upon the organism. These appropriate stimuli are called *releasers*, and the connections between them and the neural centers are presumed to be innate. These releasers are the adequate stimuli which set off the instinctive act. However, once the appropriate stimuli have released the instinctive behavior, they have no further part in the behavior. That is, the act is no longer dependent upon external stimulation and will continue even though the stimulus conditions changed completely (e.g., continuation of egg rolling by the goose even though the egg is no longer present).

The neural centers controlling the instinctive behaviors are assumed to be energy systems which have the capacity to accumulate specific energy for the act. Postulation of an energy system is made necessary by the experimental data. For example, it is known that if an act is continually repeated, eventually there comes a time when the organism does not respond even though the appropriate stimulus conditions (releasers) are present. This can be explained theoretically if one assumes that the neural-center energy system specific for that act has become exhausted because all of its energy has been used up. On the other hand, it is also known from empirical observation that, when an instinctive act has not occurred for a long period of time, stimuli which are similar to the releaser, but not the same, are capable of eliciting the instinctive behavior. At times the behavior occurs even in the absence of any adequate stimulus (called *vacuum activity*). These findings are handled theoretically by assuming that a large amount of energy has accumulated during this long time interval and that the additional energy has lowered the threshold of response so that any stimulus resembling the appropriate one will elicit the behavior. In the case of vacuum activity, it is assumed that so much energy has accumulated that it overflows its threshold and initiates the response spontaneously. It can be seen that this theory of instinctive behavior places most emphasis upon the neurophysiological factors which are genetically determined and much less emphasis upon environmental factors.

Conceptual Problems of Instinct Theories

The theorizing of Lorenz and Tinbergen has received considerable criticism on logical, experimental, and neurophysiological grounds from a number of psychologists. In addition to specific criticisms of Lorenz and Tinbergen, these writers have questioned the whole concept of instinctive behavior. Ginsberg [16] finds that eight major logical fallacies have been committed in the attempts at definition and conceptualization of instinct theories. These are failure to define what is meant by innate, use of *ad hoc* postulation to account for behavioral deviations from theoretical expectations, reasoning by analogy, attempting to explain psychological functions with biological principles while ignoring psychological principles, oversimplification of the whole problem of instinctive behavior, treating the term "instinct" as though it were a real entity rather than an abstraction, proof of instinctiveness by incomplete elimination of possible alternative explanations, and the false dichotomy of behavior into categories of learned and unlearned. Ginsberg states that behavior is a multidimensional, longitudinal phenomenon. To understand this phenomenon, one must deal with developmental continuity, not with postulated innate connections.

Following a critical examination of Lorenz's theory, Lehrman [22] points to the limitations which any instinct theory can have upon experimental investigation. His basic argument is that any theory which regards behavior as inborn, preformed, or based on specific neural structure will, by virtue of this type of "explanation," hinder or divert the investigation of these behaviors. He emphasizes that one must analyze developmental processes to understand *instinctive* behavior. In a later paper reviewing maternal behavior and the problem of instinct, Lehrman [23] rejects the approach exemplified by instinct theories and emphasizes that the approach to this problem is through the analysis of the complex developmental relationships within the animal and between the animal and the environment.

Beach [5] has also made several cogent points regarding the general problem of instinct. He states that psychologists are not widely experienced in most of these patterns of behavior. When the behavior of a given species is not actively studied or well known from a developmental point of view, a larger number of instincts assigned to that species is likely to be found. He points to the tremendous problem of behavioral classification, much of which is premature. Some of these problems of taxonomy are considered in Chapter 2.

The important point is made by Beach that the definition of a particular behavior as being instinctive is essentially a negative definition. By this he means that we must eliminate learning as a causal factor in producing the behavior before we can logically conclude that the behavior is unlearned. Psychologists have usually tried to classify behavior as learned or unlearned. The former grouping has been presumed to be defined, while the latter has included such events as reflexes, tropisms, and instincts. It should be clear, but apparently is not, that such a two-fold classification is weak. We cannot yet set the rules for what learned behavior is. It is therefore unreasonable to define instinctive behavior as unlearned. It is certain that learned behavior cannot be considered as something separate from the heredity which yields a given kind of sensory structure and nervous system upon which certain stimuli operate. Since all the facets of learning are certainly not known at the present time, it is logically impossible to classify any particular behavior as being instinctive. Beach put this succinctly when he stated that "to prove that behavior is unlearned is equivalent to proving the null hypothesis" [5, p. 405]. That is, it has to be shown conclusively that no learning has influenced the behavior under study.

Verplanck [44] has also considered and commented upon the classification of behavior into instinctive versus learned categories. He lists various criteria which have been used to classify instincts. These are stereotypy, universality of appearance, orderliness, adaptivity, resistance to modification, and execution of the behavior on the first opportunity to occur without the possibility of previous learning. Verplanck points out that many examples of learning can be found which satisfy one or many of the above criteria, with the exception of the last one. In reference to this he concludes, "We are forced into the position of acknowledging that the only criterion for distinguishing between the innate and acquired behavior is one that requires us to accept the null hypothesis as proven" [44, p. 140]. From this Verplanck draws the logical conclusion that there is no meaningful manner whereby behavior can be separated into innate versus acquired and that they should not be considered separate and different entities. From this follows "the assumption that much the same behavioral laws apply throughout the vertebrate realm (if not further)" for *all* behavior. Several consequences are deduced from this assumption. First, both learned and unlearned behavior should be controlled in the same manner by the same classes of experimental variables. Second, the theories underlying unlearned and learned behavior must turn out to be similar to if not identical with each other. Third, the particular behavioral phenomena which the ethologist observes in the field should also be obtainable by the psychologist under experimental conditions in the laboratory, and those observed in the laboratory should be observable in the field. Verplanck ends his paper with the plea that experimental psychologists expand their research to include a broader spectrum of species and also a wider range of experimental approaches, including the techniques developed by ethologists. This need is a critical one and has been stated strongly by Beach [4] and by Ross and Smith [36].

Hebb [17] has also voiced the plea that ethologists and psychologists study each other's methods and findings more carefully for the purposes of better understanding and more adequate theorizing. He, too, opposes the notion of separating behavior into categories of learned or innate, and he concludes that all behavior is dependent upon both heredity and environment and that at least all nonreflex behavior is dependent upon learning.

Two major themes can be seen running through these various criticisms. First, there is the objection to dichotomizing behavior into categories of learned versus unlearned. Second, there is the emphasis upon studying more different species over wider ranges of E and for greater periods of time. This is the point of view we have tried to emphasize in Figure 3-1.

A rather interesting approach to the learning-instinct controversy has been made by Thorpe in his book on learning and instinct in animals [42]. In his discussion of behavioral patterns of mammals, Thorpe puts forth the argument that, since it has been shown that learning is so great and so common within this class, the most reasonable first assumption is that behavior is learned. The burden of showing that a response pattern is instinctive is upon the experimenter, and until this has been done, the learning hypothesis must be considered tenable. Since the evidence available indicates continuity within nature, it does not seem reasonable to dichotomize arbitrarily this continuum at the class Mammalia and then assign two diametrically opposed hypotheses to account for behavior within these dichotomized categories, namely, all behavior exhibited by organisms below the mammalian level will be assumed to be determined by instinct until proven otherwise, and all mammalian behavior will be assumed to be determined by learning until proven otherwise.

One reason that learning appears so ubiquitous on the mammalian level is that psychologists, who are the major students of learning phenomena, have directed most of their attention to mammalian research. The learning capabilities of submammalian animals have not been explored intensively enough to specify limits and conditions of learning. The reader is referred to Thorpe's recent book [42] for a summary of much of the work which has been done. On the same topic is a paper by Hinde [19] on the modifiability of instinctive behavior in which several examples are given of instinctive behaviors that have been modified by environmental forces.

Experimental Research Concerning Instinct Theories

Current critical thinking supports the ideas that behavior cannot be divided into learned and unlearned, and that instinct, if referring to a process or mechanism independent of environmental factors including learning, is a misleading term which should be abandoned [17]. If we accept the notion that certain behaviors are unlearned, genetically determined, and independent of environmental factors, then no research will be conducted to investigate these behaviors, except, perhaps, breeding experiments. If, however, the converse is believed, then research will be done to study how environmental factors, including learning, affect these behaviors. There are several pertinent examples of research of this nature.

The work of Riess [33] is of importance first because of his emphasis upon the ontogeny of behavior. He wrote that psychologists were so concerned with developing standardized, objective measuring instruments and with formulating generalizations concerning learning that they neglected the life history of the laboratory animals which were the subjects of the experimentation. These life histories, Riess feels, are important data which should be considered in the design of experiments.

Riess's experimental work on maternal behavior in the rat is also of importance, since this behavior is usually classified as instinctive. The maternal responses in the rat usually involve the following activities: (*a*) nest building beginning a short time prior to parturition, (*b*) an increase in nest-building activity after the birth of the litter, (*c*) retrieving of young, and (*d*) suckling of young. These behaviors are frequently observed even under conditions where the female has been segregated from its mates at an early age and allowed to mature in isolation until mating. For example, Beach [3] found in a study of the effects of cortical lesions on maternal behavior in the rat that primiparous rats which had been reared in individual cages up to the time of parturition cleaned and cared for their young and prepared and fixed nests in a suitable fashion even though they had never seen nests built nor delivered litters.

Riess [32] has reported important findings concerning maternal behavior of female rats reared in cages with no objects which could be picked up or transported. The female rats were isolated in the special environment at fourteen and twenty-one days after birth. At various ages of maturity they were mated and placed in the standard test situation. The test box contained pieces of paper spaced at 1-inch distances. The major experimental group in the Riess study was reared in an environment from which all manipulatable material was removed. Powdered food was supplied in fixed food cups and because of the shape of the cup and the fine texture of the food, food handling did not take place. Water was supplied in immovable bottles. No bedding was supplied, and the cage floor was of wide-gauge mesh, so that all feces dropped through. The effects of deprivation at twenty-one days on maternal behavior at ninety days is striking. There was no nest building, decreased retrieving, and an infant mortality of 75 per cent due to the absence of suckling. The nest material was torn from the holder and carried about, but left in a haphazard fashion on the floor. The young were carried about, but they were rarely gathered into one area. Although there is the possibility of some artifactual effects (poor nutrition on the part of the mothers), the method and the rationale are of interest and pertinent to our analysis.

This study points to the difficulty of dealing with environmental factors, which may be of prime importance but are so common or ever present that their effects may be overlooked. An illustration of this is the demonstration by Von Frisch [45] of the stimulus value of the rays of the sun for orienting and communicating behavior in bees. The isolation and demonstration of this effect is one of the masterpieces of contemporary biological science.

Riess [32] has also described the work of Birch, who carried out a variation of an isolation experiment. The usual form of the isolation experiment involves an organism separated from species-mate contact for some period of time and living by itself. Comparisons are made among varying groups of isolated organisms and control (normally reared) organisms. This method makes an assumption which is of interest to consider: if the environment is kept as constant as possible, then only innate, internal, or maturational factors will operate. The effects of the stable, constant, and relatively uniform environment are liable to be discounted by the investigator.

In Birch's experiment, the actual presence of the organism in the field is one of the major variables. The isolated rat, for example, cannot be considered to be so deprived as not to experience the sensory and perceptual stimulation resulting from its own presence. Birch placed around the neck of female rats large rubber collars which were worn from infancy to sexual maturation. When the female tried to smell, lick, or manipulate her genitalia, the collar interfered with contact. In a sense the front part of the rat was isolated from the rear part. When these females delivered their young, cleaning, licking, and suckling of the young did not take place. The hypothesis of the study was that experience of the adult with its own genital sensory qualities was one determinant of the maternal behavior pattern.

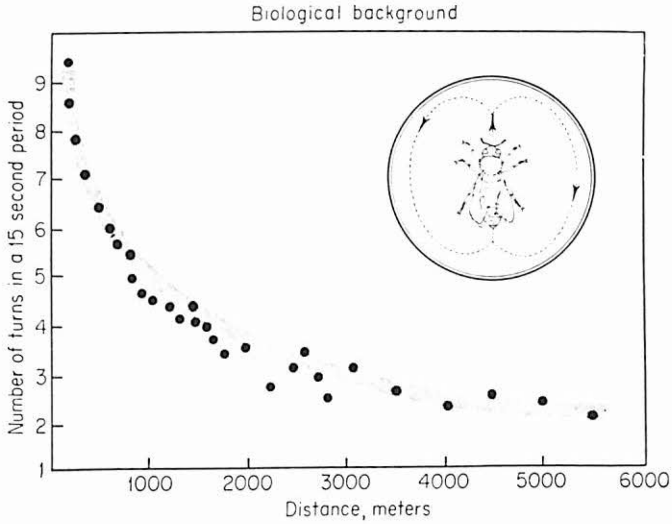

FIG. 3-4. How bees communicate the place in which they have found food. On returning to the hive, they execute a waggle dance diagramed in the inset. The speed of the dance (graph) communicates distance of food. Along the bottom of the graph is distance in thousands of meters; on the ordinate is number of turns in a 15-second period. The direction of food is communicated by varying the angle of the dance. (See Figures 9-4 and 9-5, Chapter 9.) [*Data from K. Von Frisch, Bees: their vision, chemical senses, and language. Ithaca, N.Y.: Cornell Univer. Press,* 1950.]

The two studies cited above are part of a basic attempt at analysis of some aspects of maternal behavior with special emphasis upon the isolation experiment. Two other studies are of interest in specific connection with the phenomenon of nest building in rats and in rabbits. The first, by Beach and Jaynes [7], deals with a comparison of nest-building quality and retrieving in primiparous and multiparous rats. No major differences were found in retrieving behavior or in nest-building quality when first litters were compared with later litters. In a study on rabbits, Ross, Denenberg, Sawin, and Meyer [34] found a small but significant linear improvement in the quality of nest constructed by rabbits which had produced four litters. It is clear that exceedingly basic questions remain to be answered about the behaviors involved, about the effects of environmental factors, about species differences and similarities, etc. Riess [33] has put this neatly in regard to gestational behavior in mammals. He says on page 1094:

> One is brought face to face with the fact that the parturient mother almost invariably eats the after-birth up to, but not including, the offspring. That this behavior has been found in exclusively herbivorous animals, such as the guinea-pig, suggests a basis in tissue need rather than in an ill-conceived general label of inheritance. . . . Some mothers do not stop with the placental tissue but continue to devour the young itself. Why does one find this pattern present in some mammals and absent in others, such as the fur seal, which has never been observed to eat after-birth material? The assumption that behavior of this invariant type within the species is genetically determined and "natural" for the species prevents the search for specific determinants, which may or may not be acquired as a result of experience.

The very interesting analyses of Wiesner and Sheard [46] on the effect of external (perceptual) and endocrine factors on maternal behavior is of importance here. Wiesner and Sheard showed that maternal behavior in the rat (such as retrieving) can be produced in the presumed absence of the somatic conditions usually and normally associated with maternity. These findings raise serious problems about the innateness and invariability of presumed instinctive behavior.

One of the major approaches which must be utilized in the study of innate behavior is the program of the study of the development of behavior. Lorenz [25] has said this cogently: "All living systems are, in their psychological structure, historical systems, and the understanding of all their characteristics is fundamentally impossible without insight into the historical development of the individual behavior pattern."

MATURATION

From the examples given in the previous discussion on instinctive behavior, it is clear that such patterns are not necessarily exhibited at birth, but may manifest themselves at some point in time after birth, often as late as maturity. It would seem, then, that certain events must occur prior to the appearance of these patterns which influence their development. Some of these prior events include such processes as parturition, physiological growth, neurological growth, the effects of sexual hormones, etc. The term "maturation" is used to describe those patterns which occur sometime after birth and are the resultant of normal growth and development of the organism.

Hess, has, in a recent study, presented a general statement of maturational processes as follows: "The simple fact that a behavior appears later than infancy does not necessarily mean that it is learned. It may represent the natural unfolding of innate processes occurring along with the individual's physiological development. We call this process maturation, and we may classify it as a special kind of innate behavior. Behavior which develops through maturation possesses, in all probability, the same resistance to modification that characterizes ordinary innate responses [18, pp. 73 and 74]."

Modifications of older behavioral patterns, or the occurrence of new patterns, which are brought about by learning or practice are not considered as being primarily maturational in nature. That is, the particular pattern investigated must occur in the absence of specific practice or activity to be classified as having developed through maturation. (The reader may want to refer to the definition of maturation given earlier.) This does not mean that environmental factors do not influence the development of the pattern. It does mean that specific environmental modifications are not necessary for the appearance of the behavior. Munn states that "When behavior patterns are observed to result from . . . delayed structural growth, and can be demonstrated as independent of specific environmental influences such as training or observation of the performance of others, they are . . . designated as unlearned, regardless of the age at which they appear. The process which underlies their development is referred to as 'maturation.' On the other hand, behavior produced by structural changes which depend upon specific environmental influences is said to be 'acquired 'or 'learned' " [31, p. 40].

Morgan states that maturation "refers to the completion of developmental processes within the body" [29, pp. 33 and 34], and Munn defines maturation as "growth resulting from an integral relationship of genes and their constantly changing surroundings, thus setting it off from growth as a result of exercise of sensorimotor structures" [31, p. 194].

It can be seen from these definitions that the maturational process is fundamentally related to the genetic constitution of the organism. That is, the potential for the occurrence of the pattern some time after birth is present at the moment of conception in the germal material. However, it is erroneous to think that maturation is nothing more than the late appearance of hereditary characteristics, or an "unfolding" of heredity.

To do so is to consider as inconsequential the effects of the constant parts of the environment (both intrauterine as well as external) which affect the developing organism. It also neglects the importance of the timing of environmental events which are of utmost importance in the *development* of a behavioral pattern.

The work of Riess and Birch, previously described, dramatically shows the effects of environmental modification upon two "invariant" maturational patterns. Nest building and suckling of young are two behaviors seen in the female rat when she gives birth to young. When the environment of these animals is changed so that they are not able to manipulate objects up to the time of parturition, no nests are built by the female. In Birch's study, in which rubber collars were fastened about the necks of the females, normal nursing behavior was absent.

Both of these studies point out the considerable importance of certain environmental *constancies* (the manipulation of objects and cleaning of her own body) upon the proper development of maturational patterns. When the environment is appropriately modified, the "expected" pattern does not appear.

As stated above, the particular pattern involved must not be the result of specific practice, for if so, then this is learning. The difficulty here is that not enough is known about learning to be positive that it has not occurred. If learning has taken place, then the behavior is not basically one which develops "naturally." Since it is difficult to conclude definitely that learning has not occurred, it follows that some patterns which are now considered maturational will eventually be found to be partially a function of learning, especially as our fund of knowledge concerning learning phenomena is expanded. The part of Munn's definition which states that maturation is "independent of specific environmental influences" is a definition by exclusion and demands that the complete universe of the part omitted be thoroughly known. This is certainly not true of the universe of learning.

An experimenter can, of course, utilize a particular methodology which logically eliminates the possibility of learning having occurred. Carmichael has attempted to do this in his studies of swimming in salamanders. In his first study [8], newly hatched animals which were still in a nonmotile stage were divided into two groups. One group was placed in tap water, which is an adequate medium for normal development. The other group was placed in a weak solution of chloretone, a drug which immobilizes the organism but does not interfere with neuromuscular growth. After the tap-water group had reached a behavioral level of normal swimming, the drugged animals were placed in fresh water. Within 30 minutes these experimental animals were swimming as well as the control group which had 5 days of practice in swimming. A further experiment [9] determined that the 30-minute interval between being placed in the fresh water and swimming was not a period during which rapid learning was taking place but represented the time interval for the effects of the drug to wear off. A third study [10] found that isolation from external stimulation (being placed in a soundproof, lightproof, and vibration-proof room) did not affect the swimming behavior. The conclusion from these studies was that the swimming behavior of the salamanders was unlearned and occurred after the appropriate structural development.

Here, certainly, is evidence that the behavior under investigation is not affected by practice, exercise, or learning and can be classified as being maturational when the criterion employed by the experimenter is the qualitative one of swimming or not swimming. However, a study by Fromme [14] found that when quantitative measures of swimming are used to study this phenomenon, striking differences are obtained.

Fromme essentially repeated Carmichael's study, introducing modifications which permitted him to measure speed of swimming and distance traveled. This was done by placing the animals in a narrow trough so that they could only swim in a straight line. Thus, it was possible to record the distance traversed and the time required to cover that distance. Using chloretone and tap water as the two media, he studied speed and distance swum at three points in time. These were (*a*) when the first movement normally occurs, (*b*) when the movements which just precede swimming occur, and (*c*) after swimming has developed. No differences were found between the drugged and control animals at the first stage, but significant differences in both speed and distance traveled were obtained at the latter two stages. The differences were greater at the third stage than the second. This series of studies indicates that swimming, per se, is not dependent upon experience, but that the efficiency of the swimming act is dependent in part upon prior swimming.

Space is lacking for more examples of maturational processes. The interested reader should refer to Munn [31], Carmichael [11, 12], and Stone [41] for more thorough discussions of this topic.

The investigation of maturational processes and the isolation of "unlearned" from "learned" behavior is exceedingly complex. There is a general relationship between maturation and learning in that as the animal matures, its learning capabilities are also increased. Stone [41] states in discussing this relationship that maturation always precedes and is necessary for learning and that learning generally does not accelerate or hold back maturational development. Morgan states that the function of maturation is to determine "the *rate* and the ultimate *limit* of the development of the individual's ability" [29, p. 42]. Because of the developmental changes within each of these factors, as well as the interaction between them, it may be impossible at times to separate the two variables for purposes of experimental investigation or logical analysis.

SUMMARY

We can now look again briefly at some of the previously cited studies to see the kinds of work which must be done in the study of innate behavior. We will use Figure 3-1 as a frame of reference. Some of the more thoroughly studied "inborn" behavioral patterns are those concerned with maternal behavior in rats. Primiparous rats reared under normal group conditions (one level of E) or isolated from other rats but with everything else the same (another level of E) will build nests, retrieve young, clean, suckle, and care for them at parturition (a point on the T continuum). When the female is reared in isolation in a cage in which no manipulatable objects are present (a third level of E), nest building is absent, and retrieving and suckling are markedly decreased. For rats reared so that they could not see, touch, or clean their lower body regions (a fourth level of E), it was found that cleaning, licking, and suckling of young did not take place. In all four of these studies the rats were tested at about the same point in time, shortly after sexual maturity had occurred. We have, then, the same behavior studied at approximately the same point in time but under four different environmental rearing conditions. Marked differences are obtained, reflecting the importance of certain environmental factors upon these "inborn" behavioral patterns.

The studies by Riess and Birch are part of a relatively new research area concerned with the effects of early experience upon later behavior. There is not space here to discuss these studies, and the reader is referred to the paper by Beach and Jaynes [6] for a thorough review of the literature. The general procedure in the study of early experience is to modify the early environment of the organism either by subtracting something from the "normal" environment (e.g., food deprivation, lack of visual cues) or adding something to it (e.g., shock, rich perceptual field) and then measuring the organism at a later point in time and comparing its behavior with that of a control group. One example of this approach is Hunt's study of food hoarding in the rat [20]. Hoarding can be brought about by keeping the rat on a deprivation diet and then permitting it to leave its cage and traverse an alleyway at the end of which is a pile of food pellets. Under certain environmental conditions the rat will carry back to its cage a considerable number of pellets which it will not eat. This is hoarding behavior and has been called instinctive [28]. Hunt found that rats placed on a reduced feeding schedule for fifteen days after weaning and then permitted unlimited access to food until adulthood hoarded more than twice as many pellets as controls, who had not received restricted feeding, when both groups were subjected to a hoarding test. Thus, we again see that different levels of E during one stage of development, or point in time, drastically affect presumed instinctive behavior at a later stage in development under constant genetic conditions.

In conclusion, we believe that the most effective manner of dealing with *any* behavioral variable conceptually is in terms of the suggested three-dimensional scheme. If we specify the environmental conditions, genetic characteristics, and temporal factors (including life history) of the organism, we shall be made more aware of the extreme limitations of our generalizations. This procedure should also help to avoid much of the fruitless controversy as to whether or not a particular behavior should be classified as instinctive.

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CHAPTER 4

Sensory Processes

The Methods of Sensory Physiology

It is the task of the comparative psychologist in the area of sensory physiology to determine the function of the sense organs and sensory cells that have been demonstrated by anatomical methods. The comparative psychologist has to determine the nature of the stimuli to which an animal will respond and how the animal will react to a single stimulus variable.

To obtain this information, it is obviously not feasible to use such methods as psychophysics which involve subjective reports. The inaccessibility of an animal's subjective experience forces the employment of more rigorous and objective methods in the investigation of sensory processes.

There are four basic methods used as testing procedures in comparative sensory physiology: (*a*) the measurement of the electrical activity of the neurons, called action potentials; (*b*) neural extirpation or interruption; (*c*) the measurement of learned responses; and (*d*) the measurement of innate, or unlearned, responses.

Measurement of Action Potentials. A major advantage of action-potential investigation is that we can measure sensory processes directly. However, caution must certainly be used when evaluating experimental results obtained with this method. It is possible to record action potentials in neurons leading from sensory receptors that indicate a stimulus discrimination although the animal is unable to give any behavioral evidence of the discrimination. Granit's [19] investigation of color receptors in the retina of cats with the microelectrode technique showed well-defined peaks of color sensitivity, yet there is no evidence that color vision plays a role in the behavior of the cat [22]. In other words, it looks as though an animal may sometimes possess the requisite for discrimination of certain sensory stimuli peripherally, that is, at the retinal level, but may not be able to make use of the information centrally, at the brain level. When we later discuss the specific results of various investigations, we shall have more to say about experiments involving action potential methods.

Neural Extirpation or Interruption. In order to test a hypothesis of sensory physiology, it is sometimes necessary to remove a part of the central nervous system or to sever a neural pathway. An early hypothesis on binocular equivalence suggested that the partial crossover of the optic nerve at the optic chiasma in mammals allowed each eye to have sensory representation in each half of the brain. Levine [29] cut the optic fibers longitudinally at the optic chiasma of rats but found that the operated animals still exhibited binocular transfer. It should be obvious, however, that this method will seldom give sufficient information by itself; it is usually supplemented with one of the two remaining methods to be described.

Measurement of Learned Responses. This is the most common method for determining sensory processes and capacities in organisms. The method may be adapted in a variety of ways. The classical conditioning procedure uses a natural (unconditioned) stimulus, such as food, to produce a natural (unconditioned) response, such as salivation. Then a neutral (conditionable) stimulus, such as a tone signal, is presented immediately prior to the natural stimulus. In this example, if the animal learns to salivate to the tone signal as it precedes the food, then it is possible to say that the particular tone used lies within the boundaries of the animal's discrimination. Many kinds of sensory discrimination have been tested in this manner.

Another variation on the same method is the one customarily called instrumental conditioning, where an animal has to act on the basis of a signal or cue to be rewarded or to escape punishment. The trend today is away from the use of the discrimination apparatus where the animal must move a certain distance to reach a goal; more popular now is the Skinner-box type of discrimination apparatus in which the animal may do nothing more than press an appropriate lever when the correct stimulus is presented. Failure to perform correctly in the learned-response method is sometimes taken as evidence that discrimination is lacking, but predictions based on such negative results are often unwarranted and sometimes incorrect. The animal may actually possess the discrimination ability but cannot show the ability by its behavior because the experimenter has chosen to condition a response that may for some reason conflict with the animal's normal behavior pattern.

Measurement of Innate or Unlearned Responses. One of the advantages of this method is the ease with which experiments are usually done, with respect to both the experimental apparatus and time required. Another advantage is the greater probability that one will be working within the actual response repertoire of the animal. A common example of this method is the optokinetic response obtainable in most seeing animals when a field with some sort of articulation is moved past the eyes of the animal. Usually if the animal can perceive the changes in the visual field, movements of the eye, the head, or the whole body may be observed. With this technique, visual acuity, brightness discrimination, color sensitivity, and other visual phenomena have been explored.

By knowing something about an animal's mode of behavior, we can set up experiments that yield rather dramatic results. Moericke [34] was able to demonstrate the existence of a negative afterimage for color in the peach aphid. He noted, first, that the peach aphid would make stabbing movements to penetrate the substrate only if it was placed on a field of green color. With this knowledge, he exposed aphids for some time to a complementary color of green, then placed them on a neutral gray substrate and found that the aphids would make the penetrating movements, although they would not normally do this on gray substrate. We could hardly ask for better evidence of negative afterimages in these animals. Similarly, by taking advantage of the known fact that newly hatched chicks prefer a desaturated but colored object over one that is achromatic, Gogel and Hess [17] were able to show color constancy in chicks that had had no previous visual experience. The unlearned response taken advantage of here is the tendency of visually naïve chicks to peck at what appear to them to be food objects.

Experimental Determination of the Variables of Sensory Process

We may define stimuli as the extremely small energy changes that initiate, or steer, activities of the organism. These energy changes are received by the specialized receptor organs or the general sensitivity of unspecialized cells. In single-celled animals the information of energy change goes directly to the effectors; in higher animals the information is first relayed to the central nervous system. Reception of the stimuli involves an absolute level of energy, its temporal duration, and its quality.

Absolute Energy Levels. We have already said that the amount of energy needed to activate a receptor is extremely small. Some receptors have such a low absolute threshold, the energy level at which a receptor will first respond, that it is difficult to imagine how they could be more sensitive and still maintain adequate performance. The absolute threshold is about 4×10^{-17} watt for the human ear. If the ear were more sensitive than this, we should have the problem of a constant sound produced by the Brownian movement of air molecules. The conclusion should not be drawn from this example that man has primary claim to this degree of receptor sensitivity. It has been estimated that the minimal stimulus value for the subgenual (auditory) organ of the cockroach is about 6×10^{-17} watt.

Temporal Energy Durations. In order to say much about minimal stimulus energies we must introduce the factor of time. A minimal stimulus must endure a certain length of time to cause a reaction. The time necessary for a stimulus to cause a reaction in the human eye is about ½ second at threshold, so that we have the following statement about the eye and the ear of man: eye, 2×10^{-17} watt-second; ear, 3×10^{-17} watt-second.

Besides the minimal stimulus time necessary for a reaction, it is also necessary that stimuli endure long enough to be perceived as discrete events. The shortest times that can be perceived as time are quite long. Durations of time shorter than 1/20 second cannot be separated. For example, flashes of light appear equally long when *equal stimulus energies* are presented to the sense organs. It is impossible to distinguish between stimuli of 5 and 40 milliseconds, in terms of duration, when the shorter one is correspondingly eight times more intense. This is known as the Bunsen-Roscoe law: $I \times t = k$, where I = intensity, t = time, and k is a constant. The law does not hold for some exceptions, for while there is a lower limit for the perception of time, there is none for a short stimulus if the intensity is increased to a sufficiently high level. In other words, a flash of light which endures for a millionth of a second can easily be seen if the intensity is at a sufficiently high level.

Quality of Energies. Sensory receptors are adapted for specific kinds of energy. It should be kept in mind, however, that for a given sense organ, there is an optimum within the perceptible stimulus range. For example, the human eye is most sensitive to light waves of about 507 millimicrons, which is in the green range of the visible spectrum. This means that one may detect the presence of a light of this color at a lower intensity than lights from other parts of the visual spectrum.

VISION

It has been said that nearly every type of eye imaginable from the engineering viewpoint has been developed by some animal. At the higher levels of development, which include all image-forming eyes, there seems to be no particular improvement of the visual process, except possibly in the primates. Compared with man, birds have better acuity, bees can see wavelengths invisible to us, and other insects have a much faster recovery rate. Even the lens-type eye is not confined to vertebrates but shows up in the invertebrates, although in a somewhat different form, particularly in the cephalopods. We can demonstrate the extreme diversity of visual organs by referring to the size of the lens in the eyes of several animals. In some of the smaller rodents the lens may be as small as 0.3 millimeter in diameter compared with 16.2 millimeters in man, while the whale has perhaps the largest of the mammalian eyes with a lens diameter of 40 millimeters. However, none of these compares with the tremendous eye of the giant squid, in which the lens has been measured at 300 millimeters, and may be even larger in some specimens where it has been difficult to obtain actual eye measurements.

Among many different types of eyes that have developed, it is possible to find variations on a single theme. There are foveas present in many retinas, and some birds have two, one that is used in binocular vision and one that is used in monocular vision. A means of increasing sensitivity is by increasing the number of rods. Some animals have maximized their sensitivity by large pupils and large lenses; the lens of the mouse and opossum fill a much greater proportion of the eye than the lens of man. Another phylogenetic trick is the tapetum. This is a kind of reflecting substance in the back of the retina which permits the light to be reflected back and forth in the eye. Accommodation, one of the important mechanisms for perceiving depth, is achieved in fishes, amphibians, and snakes by moving the lens toward and away from the retina; in birds, reptiles other than snakes, and mammals, the lens changes shape. The amount of accommodation varies over a wide range: in man and the domestic chick it is about 10 diopters, in the cormorant up to 50 diopters, and in the turtle as much as 100 diopters.

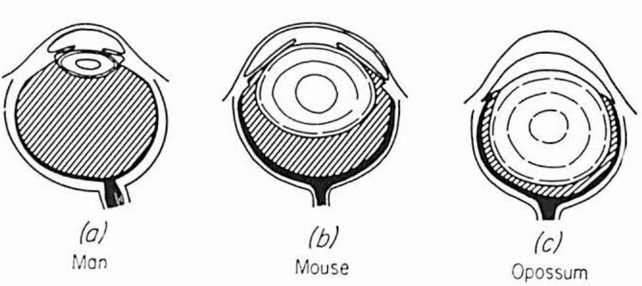

FIG. 4-1. Eyes of mouse and opossum compared with those of man. Note large lenses in mouse and opossum eye. [*From W. Von Buddenbrock, Vergleichende Physiologie.* 1952, **1**, 129, *fig.* 71.]

An unusual visual organ, the pineal eye, is found in some fishes and in some lizards, as well as in the tuatara, a lizardlike reptile, where it is well developed. The third eye has little functional significance. Increased light on the organ is known to affect rate of breathing.

Diffuse Sensitivity to Light in Lower Animals

Many organisms are able to react to light by means of a diffuse sensitivity. Amoebas are sensitive to light anywhere on the body; because of the periodically fluid state of its protoplasm, the light probably affects the animal through its sol-gel reversibility. Annelids, worms with segmented bodies, also are light sensitive throughout the body surface, but they have regions of maximum sensitivity which coincide with epithelial light cells, a simple form of single-cell receptor consisting of a refractile body and neurofibrilla.

Local Sensitivity to Light in Lower Animals

Localized receptors that are responsive to intensity can be found in the flagellate protozoan. In *Euglena*, a mass of red granules called the stigmata is located next to the flagellum; light affects the change in swelling of this structure and thus causes a change in the direction of beat of the flagellum. In another protozoan the stigma is a cup-shaped mass of pigment covered by a refractile structure which serves as a lens. Another type of light receptor called the ocellus may be as simple as the layer of sensory and pigment cells found in coelenterates or as complex as the eyes of some mollusks, which rival the vertebrate eye in complexity of development.

Sensitivity to Polarized Light

Although it is not very common, there are indications that a number of animals have the ability to see polarized light. The most famous work in this line was done by Von Frisch [48], who discovered that bees could see the polarized light of the sky and use it as a means of orientation. Crustaceans have been observed to swim in the plane of polarization and must therefore be able to see polarized light. The only higher animals that have been demonstrated to have polarized-light vision are some of the large wading birds, such as herons. In the latter case the mechanism may simply be used for killing the glare on the shallow water in which they wade. This has, of course, the effect of removing surface glare in such a way that prey can very readily be seen in the shallow waters and then seized by the bird. It would be very similar to our using polarizing filters for photographing objects in the water or using polarizing sun glasses to be able to see better in areas of high reflection.

Brightness Discrimination

Brightness discrimination is perhaps the most universal visual response in the entire phylogenetic scale. It has been determined for most organisms down to the protozoans, and some quantitative work has been done, particularly with marine invertebrates. Essentially we can say that there is no real improvement in brightness discrimination as one progresses up the phylogenetic scale and that variations in the ability to discriminate among different brightnesses more likely represent inadequate measuring techniques.

Visual Acuity

Experimental investigation of visual acuity has often been carried out by means of the optomotor method, although training techniques have also been utilized. According to Walls [49], a number of animals at the higher vertebrate levels show essentially small variation in their ability to discern small stimuli. The angle which can be discriminated by man is about 64 seconds, by the chimpanzee 47 seconds, and by the rhesus monkey 67 seconds. These measurements, of course, are in terms of minutes and seconds of arc. Actually, this does not mean that man is near the peak of ability as far as visual acuity is concerned. As we have said earlier, many birds are able to far exceed man's capacity for visual acuity. The visual acuity of most invertebrates is correspondingly less, owing mainly to the type of eye possessed by these animals. It is possible to make the general statement that the lower vertebrates on the whole have poorer visual acuity than the higher animals. This is undoubtedly due to the variation in the number of sensory receptors per unit area in the respective vertebrate eyes. In most of the nocturnal animals, acuity is much poorer. For example, Walls indicates the following: cat, 5.5 minutes of arc; alligator, 11 minutes; opossum, 11 minutes; rat, 26 minutes; and white rat, 52 minutes.

Form Vision

Form vision is undoubtedly absent in many of the lower invertebrates because of the structure of the visual system. In order to perceive form, there must be an adequate sense organ to produce an image which can be subsequently discriminated. A possible exception is the form vision possible in some of the insects, where the faceted eye seems to be capable of discriminating at least certain types of forms. For example, bees can be trained to discriminate a five-rayed star from a square or a circle. This does not necessarily mean that form vision per se is involved here. It has been shown that the amount of flicker produced when the faceted bee eye passes near the articulated object is greater than that for the more solid object, and discrimination may rest merely on this difference of flicker which is perceived by the animal.

In the vertebrate series, where the eye is relatively the same in all species, form vision has been shown to exist from the fish to primates. Although form discrimination per se has been denied in the lower vertebrates by some investigators, the problem is perhaps merely a theoretical one. Bingham [7], for example, insists that the ability to discriminate a circle from a triangle in no way implies form vision on the part of the animal, but rather that differences in detail of stimuli are perceived. In other words, the concepts of triangularity and of circularity as such do not enter.

Probably the answer again lies in the methodology used for testing the pattern of form discrimination. Lashley's [28] experiments with the jumping stand are a good case in point. Before his technique was developed, it was generally considered that the white rat was incapable of discriminating form. However, using the jumping-stand technique, Lashley found that the animals could easily be trained to make discriminations which were quite in line with what usually is considered to be form vision in discrimination experiments. Similarly, the cat has been considered to have relatively poor form vision. However, in order to test for certain theories of perceptual organization, Sperry [41] was recently able to teach cats form discrimination of a complex nature. In fact, his cats were able to make discriminations of patterns which varied so slightly that the actual concept of form vision certainly must be included under the results he obtained.

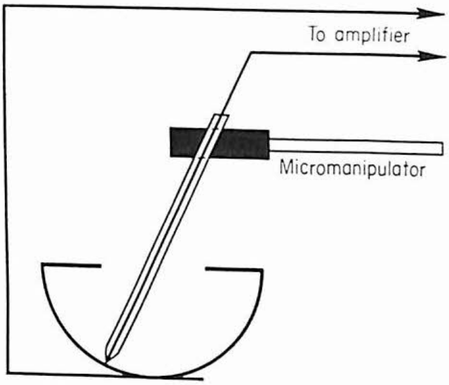

FIG. 4-2. Diagram of excised, opened frog eye with microelectrode inserted to record electrical impulses produced by various light stimuli. [*From Ragnar Granit, Sensory mechanisms of the retina. London: Oxford, 1947, p. 348, fig. 175.*]

Color Vision

Of all the visual processes studied in animals, color vision has for some reason held the most fascination for a great many investigators. Probably more has been written on color vision in animals both in the scientific and the popular press than on any other visual process. The perennial article in the hunting and fishing magazines as to whether or not fish are color blind and speculation as to whether the bull can really see the red flag are cases in point. Actually, there is a lot of good work, much of it in the German literature, which clearly indicates the presence of color vision in at least some animals all the way through the phylogenetic scale. By use of the training techniques, almost all the higher vertebrates as well as some of the higher invertebrates, as cephalopods and insects, have been tested for color vision.

In more recent literature, there is an increasing amount of work reported which deals with electrophysiological methods. Electroretinograms as well as microelectrode work is reported. Granit [20] has carried analysis of color vision to a fine point by means of these electrophysiological techniques. There are also other methods which can be used. We have already discussed innate movement responses. It is quite possible, for example, to use the optokinetic nystagmus response, which is a reflex of the eye to track movements, as an indicator for color vision by using colored stripes and different shades of gray stripes in an optokinetic apparatus.

It is also possible to assume color vision when animals that change color are tested in their chromatic adaptation to various color substrates. Certain fishes, crustaceans, and cephalopods change color to adapt to the particular background on which they may be resting. By systematically varying the color of the background and then studying the action of their chromatophores, we can conclude that color vision exists, since the responses change according to changes in the background. In some experiments on color preferences of newly hatched chicks, it was possible to determine color vision in visually naïve animals. By varying brightness and saturation, it was possible to arrive at some notion of the color preference and sensitivity of the newly hatched chick [24]. A similar technique has been used in another instance where the innate pecking response of chicks and ducklings to colored stimulus objects has indicated the natural preferences of these animals [25].

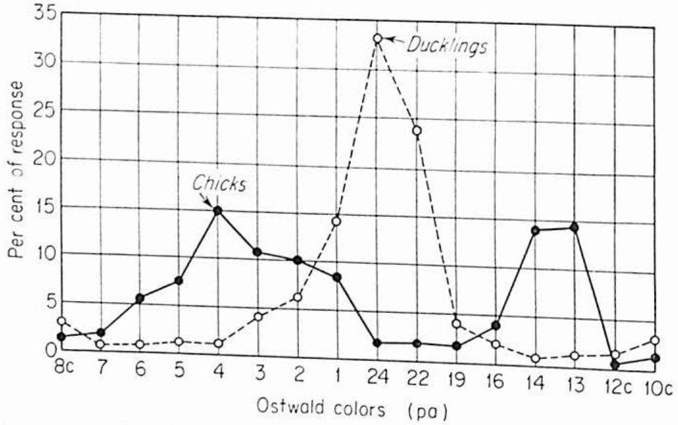

FIG. 4-3. Percentage of total pecks delivered by inexperienced chicks and ducklings to each of sixteen colors, using a natural preference apparatus. [*From E. H. Hess, Natural preferences of chicks and ducklings for objects of different colors. Psychol. Rep.,* 1956, **4**, 481.]

While the biological meaning of color vision is quite clear when we consider animals such as the bee, which is dependent on flowers as a food supply, there is some question as to its biological usefulness in many other species. In various flies, frogs, or turtles it is not so simple to recognize the biological utility of a well-developed color sense. The general distribution of color vision in the phylogenetic scale is essentially limited to the vertebrates; and of the invertebrates only the arthropods and the highest mollusks (cephalopods) seem to have a color sense.

Color Vision in Insects. Color vision in insects seems to be almost universal in distribution but is by no means found in all species. There also exists no real correlation between the biology and behavior of the animals and the presence or absence of color vision. For instance, some insects which visit blossoms of flowers may be color-blind, while other insects which, for example, feed on dung may be quite capable of good color discrimination.

One of the classic arguments in the extensive literature of color vision deals with the presence or absence of color vision in bees. Von Frisch [44], however, in 1914 was able to show the color sense of bees beyond any doubt, and at that time he developed the so-called "checkerboard technique" for the investigation of color vision in the bee as well as in other insects. The essential technique is illustrated in Figure 4-4, and the process is as follows. Bees are trained to come to a small glass container in which there is a certain amount of sugar water. This container rests on a sheet of, say, blue paper. After the bees have been thoroughly trained for several days to come to this container, a number of pieces of paper are now substituted, one of which is the original blue paper and the others are grays ranging from white to black. These pieces are arranged in a checkerboard pattern. The blue paper is somewhere among the various grays. Clean glass containers are now placed, one each, over the various pieces of paper, and the number of bees going to the different containers is counted. In the experiments with bees, many more bees go to the container on the blue background than on any one of the grays, and therefore blue sensitivity is established. If a solid red is used for initial training and the same checkerboard technique then applied, there will be some bees going to the red paper, but also many will go to the black and the very dark grays. This not only indicates an absence of color vision for red but also gives some notion as to the relative brightness of that color as it is perceived achromatically by the bees. On the whole, as we have indicated before, color vision in insects is not a clear discrimination of a number of colors but rather a matter of distinguishing between

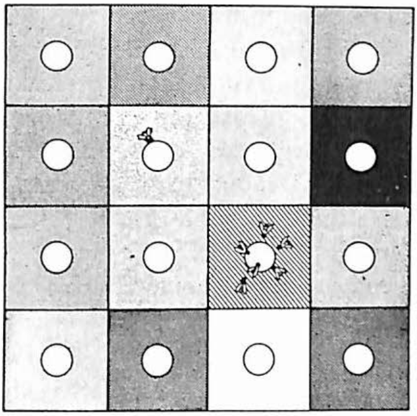

FIG. 4-4. Checkerboard technique for testing color vision in bees. Bees trained to collect food from a container placed on blue paper congregate on the blue square, proving that they can distinguish this color from the various shades of gray. [*From Karl Von Frisch, The dancing bees. New York: Harcourt, Brace,* 1955, *p.* 77, *fig.* XIV (6).]

groups of colors, and in most cases this is two rather than the four regions of discrimination shown by the bee.

Some electrophysiological work has also been done in color vision of insects. Autrum [5] used the method of color-flicker photometry and came to the conclusion that there were at least three different kinds of color receptors in the eyes of the insects he investigated. Tsuneki [42] reported that two species of ants showed discrimination or relative sensitivity to various monochromatic lights, but he was unable to show color learning. He suggested that the result indicated that the ant has color vision but cannot associate color with any of the particular behavior in which it engages. This is a problem in much of the color-discrimination work done in animals.

Color Vision in Mollusks. We know almost nothing of the color sense of snails and most other mollusks, but we have information regarding the color vision of cephalopods. Kühn [27] investigated the color vision of squids by means of training techniques, using the association of color and punishment. In this way it was possible to demonstrate color vision; he also demonstrated color vision in *Sepia,* in which the chromatophore change in the animal when exposed to various color substrates demonstrated the existence of color sensitivity.

Color Vision in Vertebrates. As we have indicated earlier in this chapter, the vertebrate eye is characterized by two different kinds of light receptors. The more sensitive elements are the rods, while the cones are assumed to mediate color vision. Throughout the animal scale in the vertebrate series, there are cone retinae, rod retinae, and mixtures of both. The latter are the most common. The duplicity theory, which was formulated by von Kries in 1896, indicates that rod retinae are used primarily by animals who are nocturnal and that cones are used for color vision and therefore would be essentially the property of diurnal animals. One argument for the duplicity theory is the so-called "Purkinje effect," which is a difference in the apparent brightness of spectral color under conditions of light and dark adaptation. A shift in maximal brightness toward the short wavelengths of the spectrum under conditions of dark adaptation can be explained only in terms of two different receptor systems which operate under these two conditions of illumination.

The Purkinje phenomenon has been demonstrated to exist not only in humans but also in a number of lower animal forms. It has been found in fishes, frogs, alligators, various birds, and a number of mammals. It seems to be missing in the receptor systems of animals that seem to have only one type of receptor, as in the turtle with its pure-cone retina. Von Frisch [45] was able to show that in fishes there was an actual movement or migration of some of the sensitive cells and pigment in the retina which allowed for light and dark adaptation and in which condition he could histologically recognize rods and cones. He was able to show that the color discrimination which the fish had readily learned was impossible when, because of a lower level of illumination, the cones had moved away from the retinal plane and the rods took over. At any rate, this study is evidence for the duplicity theory and is also one of the earlier studies in which color discrimination in fishes was adequately shown. These are just some examples of the problems of color vision as they are to be found in all vertebrates.

In the determination of color vision in vertebrates, the various techniques already discussed in this chapter have been used. In addition, there has been an attempt to determine color sensitivity of animals by means of measuring the amount of pupillary contraction which occurs when the eye is stimulated with wavelengths of low energy, but these results, on the whole, have been less satisfactory than those obtained by the more standard techniques of discrimination learning.

The capacity of fishes to see color has been doubted for a great many years. Contributing to this belief was the general assumption that colors lost their quality in water. In other words, it was believed that fishes in even a reasonably shallow depth would be unable to see color, since red and yellow wavelengths are almost completely absorbed and, as a result, the color changes into a kind of greenish monochrome. However, experimental findings show that up to a depth of 100 meters there is reasonable opportunity for the fish to discriminate color. Von Frisch [43] introduced two techniques for the study of color vision in fishes: the first was concerned with determining the adaptation to a color of the substrate, and the second involved learning and discrimination experiments with colored food. The former technique was subsequently used by Mast [31] when he worked with various flat fishes to investigate adaptation to colored backgrounds. After that came a great many experiments which dealt with color vision in fishes and were mainly carried out by means of the training (reward and punishment) technique.

A number of similarities have been found between the vision of fishes and of man. For example, the law of complementarity is demonstrable at the fish level. One difference that is essentially apparent in the color vision of fishes is that they are able to perceive ultraviolet light, presumably as a color. Color vision is most highly developed in the teleost fishes, and it is probably absent only in those that are primarily nocturnal and depend to a greater degree on chemical sensitivity than on visual recognition of food objects.

The color vision of amphibians has been investigated mainly during the past several decades. An earlier attempt was made by Babák [6], who investigated the changes in breathing rhythms of a frog under the influence of various color illuminations. The actual experimental procedures involving discrimination learning were carried on by a number of investigators, but mainly with optomotor and electrophysiological techniques. By these methods it was found that the frog *Rana temporaria* had the ability to differentiate red from blue but was unable to differentiate green from yellow. Granit's [18] results, however, indicate that the color vision system of the frog is similar to that of the human, a result which is not coincident with the earlier findings. Birukow [8] also has studied the optokinetic development of color vision in *Rana temporaria*. Color vision in the developing frog tadpole has been investigated by optomotor experiments complemented with histological examinations. It was shown that cones appear first and become capable of functioning. Color differentiation in this early stage, however, is not possible. It appears only in stage two for the color blue and in stage five for red, at which time the hind leg is completely developed One last item in the color vision of amphibians is that their visible spectrum, particularly in frogs and toads, extends into the ultraviolet region. Zipse [52] found that these animals are able to feed in complete ultraviolet light.

Table 4-1
Phylogenetic Developments in Vision

Class	Representative animal	Organ	Development
Sarcodina	Amoeba		Diffuse sensitivity to light
Oligochaeta	Earthworm	Epithelial light cell	Localized sensitivity to light
Cephalopoda	Nautilus	Ocellus	Possible pattern vision
Insecta	Bee	Ommatidium	Color vision
Osteichthyes	Goldfish	Retina	Color vision
Aves	Falcon	Retina	Superior visual acuity
Mammalia	Cat	Retina	Light reflective tapetum
Mammalia	Primate	Retina	Double retina

Color vision seems to be present in those reptiles which have been investigated, with the exception of species that are essentially nocturnal. The microelectrode technique has demonstrated sensitivity for green and red in snakes. The training techniques have been used very little, if at all, in snakes, but they have been used in turtles. In addition, other experiments done with electroretinograms indicate that there is good color vision. This method has shown that the turtle, *Pseudemy*, has both photopic (cone) and scotopic (rod) retinal mechanisms.

All diurnal birds seem to have a highly developed sense of color vision. In most instances it appears to be quite similar to that of man, although general sensitivity in the short end of the spectrum is less than that in the long end. Pupillary responses to various wavelengths of light have been recorded also by Erhard [13], who used over forty species of birds.

In Erhard's data, only the owl has a high sensitivity in the green and blue area of the spectrum, a fact which of course fits the rod retina of the owl. Another interesting technique dealing with color sensitivity in birds was that developed by Henning [23], who used colored glasses on pigeons. He found that when he used red or yellow glasses on the pigeons they were able to get back to their homes very quickly but that with green and particularly with blue glasses the birds either had difficulty finding their way back home or would be completely unwilling to fly. However, this does not necessarily mean that the birds are insensitive to blue but rather, less sensitive.

Table 4-2

Relative Brightness Matches for Colors of Different Wavelengths, Using Differential Pupilloscope

(The maximum figure indicates the part of the spectrum to which the eye is most sensitive.)

Spectral light	Man	Chicken	Rose cockatoo	Herring gull	Kestrel falcon	Wood owl
Red	7.9	31.6	40.0	20.4	8.8	1.7
Orange	16.5	40.0	40.0	21.4	23.7	8.3
Yellow	20.4	40.0	40.0	25.0	40.0	37.8
Yellow green	29.8	12.4	16.5	11.8	22.4	37.8
Blue green	18.4	4.8	4.8	6.9	14.0	23.7
Light blue	13.2	1.8	1.8	5.4	7.3	21.4
Blue	2.6					

SOURCE: From H. Erhard, Messende Untersuchungen über den Farbensinn der Vögel. *Zool. Jb. Abt. Allg. Zool. Physiol.*, 1924, **41**, 489–552.

There is very little question but that the color sensitivity of mammals compared with the rest of the vertebrates is rather poorly developed. One possible reason for this is that many of the mammals are primarily nocturnal animals and depend also to a greater extent than most vertebrates on the sense of smell. A really well-developed color sense comparable to that of the human is found only in the primates. Almost all other mammals have a very poorly developed color sensitivity, although Adrian [1] has determined that the light-adapted guinea pig eye functions as though it uses cone vision. Quite recently Arden and Tansley [3] by means of electroretinograms found that there was good color sensitivity in the pure-cone retina of the gray squirrel. They found further that there is no Purkinje shift, which fits in well with what we have stated before regarding this phenomenon. The color vision of rats, mice, and rabbits seems to be so poor that it can be considered absent.

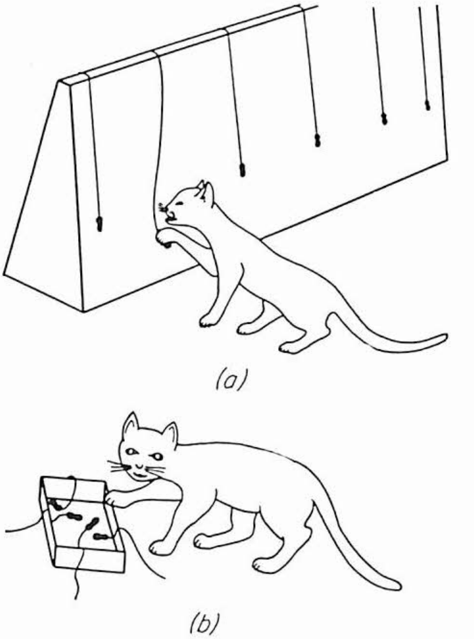

FIG. 4-5. *a.* Choice board: cat chooses model of proper color. *b.* Choice box: cat retrieves the model of the color which will induce the experimenter to engage in play. [*From Christiane Buchholtz, Untersuchungen über das Farbensehen der Hauskatze, Felis domestica L. Z. Tierpsychol.*, **9**, 464–465, *figs.* 2 and 3.]

The problem of the cat, which ordinarily is classed with these other animals, is, however, somewhat peculiar. In fact, a spate of studies in the last ten years has produced some contradictory results, but certainly the weight of all the evidence is along the line that the cat does not have color vision. Some of the studies, primarily Gunter [22] and Meyer, Miles, and Ratoosh [32], indicate no color vision in the cat. However, Bucholtz [9], using an entirely different technique, found indications of fairly good color-vision discrimination in cats. She used the reward of allowing the cats to play with a colored model which was moved by her and found that the cats were able to discriminate this model from any of a large series of neutral gray models. However, there is little question that the cat has perfectly good color receptors in the eye but apparently no ability to use these color perceptions in the brain. Conflicting reports on the dog probably fall in this same category.

AUDITION

Sensitivity to Vibration and Sound in the Lower Forms

For some years it has been the practice to attribute sound sensitivity only to those animal forms having receptive structures homologous to the human ear. This is not very logical. The proper definition of hearing is the awareness of vibrations in an elastic medium. A sound that is airborne is not qualitatively different from a sound that is water- or earthborne.

There is a little evidence that hearing is present in phyla below the arthropods. Some of the worms are certainly sensitive to substrate vibration, with reception mediated by the touch receptors. No other sense, however, has appeared as abruptly on the phylogenetic scene as hearing. Even vision had its forerunner in the light-sensitive cells and tissues of lower forms, and the chemical senses are part of any life form. Hearing, by the definition currently in use, appears at the vertebrate level, and even there tremendous changes are found from fishes to the mammals which are unparalleled in the development of any other sensory system of organisms.

Auditory Receptors in Insects

Insects have been the most thoroughly investigated of the arthropods for auditory processes. We now have enough data to know that insects are sensitive to airborne sounds and, moreover, that some of them employ ultrasonic frequencies for communication.

There are two different types of receptor organs involved: one comparatively simple type for low frequencies and a more elaborate type for communication at high-frequency levels. The simpler organ is composed of hair sensilla. On the base of each hair rests a dendrite of a sense cell. The hair and the cell as a unit has a remarkably low threshold. Using an oscillator as stimulus and an oscillograph to record the nerve impulses, Pumphrey [38] has investigated the hair sensilla of the cricket, cockroach, and locust. He was able to show that the sensilla are so sensitive to air currents that it is likely that the ever-present neural activity is caused by excitation of the end organs by Brownian movement of molecules. Minnich [33] decided by watching the innate reaction to sound that the upper-frequency limit for hairy caterpillars of *Vanessa antiopa* is about 1,000 cycles per second, while the lower limit extends below 32 cycles per second.

The second type of receptor is usually called the tympanic organ. Unlike the hair sensilla it is limited to a few species. Anatomically, it may be located in different places; it may occur in the abdomen, as in the grasshopper, or in the legs, as in the cricket. Regardless of where it is located, it is essentially of the same morphological nature. Typically there are paired slits in the exoskeleton; the cavity behind each slit forms the tympanal duct, and each cavity ends on a thin membrane which functions in much the same way as the human eardrum. On the inner side of the membrane is an air sac, with the effect that the membrane can act as a lever. One end of the membrane is anchored to the exoskeleton, while the other is fastened to the so-called "chordotonal organ." The latter generally consists of a distal cell, one end attached to the tympanum and the other surrounding the sense cell. Relative movements between the distal and sense cells serve to stimulate the latter.

The frequency range of tympanic organs in insects differs from species to species but in all cases is high, and the upper limit is almost always beyond the boundaries of human hearing. The threshold for intensity is low; in the Acridiidae it is not much higher at 10,000 cycles than for man. The tympanic pits act as localizers, so that localization in space is also reasonably good.

A perplexing question has concerned the pitch discrimination of the tympanic organs. Structure precludes the organ from being anything but a poor harmonic analyzer, and the experimental evidence for frequency discrimination is slight. Yet the behavioral evidence strongly implies that insects can distinguish calls of their species from those of other species or from artificial sources. Pumphrey and Rawdon-Smith [37] have suggested a solution to the problem. Again using their electronic apparatus, this time connected to preparations of the tympanic organ and auditory nerve of a locust, they discovered that while there was a lively response to a pure tone of 8,000 cycles, the response was random, therefore denying discrimination of pitch. But when this carrier tone of 8 kilocycles was modulated at any frequency up to 300 cycles, it was immediately evident that the neural discharge matched the modulation frequencies. With further information of this sort, it was possible for the researchers to advance this suggestion: the high-frequency tones to which insects respond are meaningless in themselves; what is important is the detection by the tym-

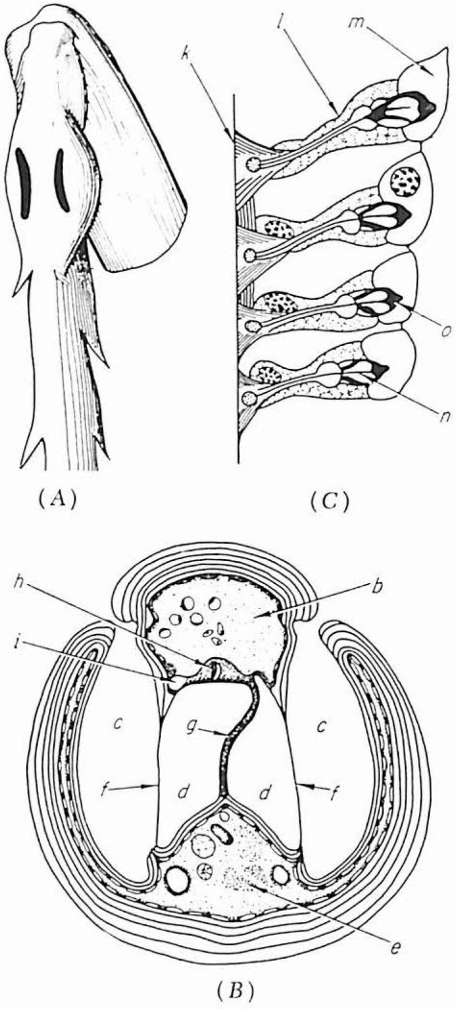

FIG. 4-6. Tibial tympanal organ of locustids: (*A*) surface view; (*B*) transverse section of anterior tibia of *Decticus* at the level of the tympanal organ; (*b*) blood channel, (*c*) tympanal cavities, (*d*) tracheae, (*e*) blood channel, (*f*) tympanum, (*g*) rigid wall between tracheae, (*h*) crista acoustica with one chordontonal organ, (*i*) sense cell; (*C*) longitudinal section through a part of the crista showing chordontonal organs; (*k*) trachea, (*l*) sheath cell, (*m*) cap cell, (*n*) axial filament, (*o*) apical body. [*From K. D. Roeder (ed)., Insect physiology. New York: Wiley,* 1953, *p.* 535, *fig.* 139.]

panic organ of the lower frequencies riding the carrier frequency. This is quite unlike the process employed by the human ear, but it is the same principle used in the transmission of radio signals.

Song patterns in the grasshopper genus *Chorthippus* have been studied by Faber [14], who was able to discriminate up to twelve different sound patterns or phrases, each of which was the result of a particular emotional situation in the grasshopper. His work has since been continued by a number of investigators, particularly at the University of Munich, and hybridization experiments between two species of crickets have been carried out. Interesting hybrid songs have been the result of some of these experiments.

Autrum [4] also worked with the hearing of insects, using electrophysiological techniques. He was able to determine an upper-frequency response up to 90,000 cycles in two species of grasshopper. An interesting additional finding of Autrum's was that the sensitivity of the hearing system in the grasshopper is highly dependent upon temperature, with a maximum sensitivity at about 30° C.

The Hearing Organs of Fish

Insight into the evolution of hearing in fish is best had by recalling that a fish has nearly the same compressibility and density as the medium surrounding its body. It is thus easy to see how an object moving close to the animal will maximally deform its body surface. Any organ, then, capable of perceiving deformation or touch could become specialized in localization of distant disturbances. It could become further specialized if the whole organ were innervated from one source so that simultaneous comparisons could be made.

This development of a sound-receptive organ from tactile organs has been achieved in fish. The lateral line is a system of receptors present throughout the surface of the body, with concentrations of the receptors forming a line running along each side. Sensitivity is extremely high, but the system as a whole is one of limited range. Reception is confined to the lower frequencies; the 300-cycles figure set by Parker and Van Heusen [39] for the catfish seems representative of the upper limit. There is no pitch discrimination. The system has other defects too, inasmuch as it cannot provide a moving fish with a spatial reference point for sound. These defects in the lateral line organs have been met by the evolution of compensating organs. The utricle filters out the effects of gravity and linear acceleration, while the semicircular canals, responsive to angular acceleration, completes the filtering process.

Concomitant with the development of the utricle has been that of the sacculus and the lagena, which together provide a wider coverage of frequencies and add quality discrimination.

The lagena, found in most fishes, is a small evagination of the sacculus. It is served by a separate branch of cranial nerve VIII, as is the cochlea of mammals. The lagena, in fact, becomes progressively larger in amphibians, reptiles, and birds until in mammals it has become the cochlea proper.

There is no middle ear in fish, and the Weberian ossicles, forerunner to the middle-ear bones of mammals, are embedded in tissue. The ossicles are connected to the air bladder, an excellent pickup for sound waves, from which they transmit sound to the sacculus and lagena. This structure is not present in all the fishes but has been studied in a number, particularly in carp.

The upper limit for the sacculus and lagena varies from species to species. Some of the variation is likely due to differences in technique. Von Frisch [46] obtained responses from minnows at 5,000 to 6,000 cycles. Conditioned-response experiments have left no doubt that fish have good pitch discrimination due to the existence of the lagena.

Hearing in Amphibians

The principal development of the auditory end organ from the fish to the amphibian is that of the middle ear in the latter. The Weberian ossicles in fish have given way to a bony rod called the *columella* that connects the inner ear to the eardrum. In the early stages of the tadpole, the columella is a bridge from the round window to a part of the lung sac, reminiscent of the air-bladder connection in fish. In latter stages of the tadpole's existence the so-called "aortic columella" disappears, heralding the transition from a purely aquatic life to an amphibious one; and another columella, the tympanic, grows in the middle ear from the oval window to the eardrum.

The old Yerkes [51] experiment showing a frog's hearing range to be from 50 to 10,000 cycles still stands, but not because the result has been confirmed. Auditory experiments in amphibians have been sparse. This is unfortunate, since the phylogenetic history of sound reception cannot be complete without further knowledge of the hearing of these animals that bridge the gap from water to air.

The Hearing Ability of Reptiles

Manning [30] has produced evidence that rattlesnakes do not hear airborne sounds. Snakes have no middle ear and the columella, rather than being attached to a tympanic membrane, is fastened to a bone on the skull so that ground-borne, rather than airborne, vibrations are the most likely to be heard.

In other reptiles, especially alligators, crocodiles, and lizards, the auditory organ has evolved considerably beyond the attainment of the amphibians. The crocodile and alligator have a fold of skin above the ear opening which could be called a rudiment of an external ear. In the alligator, at least, the lagena has undergone a change to form three ducts of the inner ear and the basilar membrane. Except for snakes, the columella has also changed and is now formed of two bones. Hearing ability, where it exists at all in the reptiles, has often been brought to question.

Table 4-3
Phylogenetic Developments in Hearing

Class	Representative animal	Organ	Development
Insecta	Cricket	Hair sensilla	Sensitivity to airborne sound
Insecta	Locust	Tympanic organ	Frequency discrimination
Osteichthyes	Catfish	Lateral line	Sensitivity to change in pressure
Osteichthyes	Goldfish	Sacculus and lagena	Frequency discrimination
Reptilia	Alligator	Inner ear	Three ducts
Aves	Parrot	Cochlea	External auditory meatus
Mammalia	Rat	Cochlea	Three ossicles

In turtles, for instance, Wever and Bray [50] found a microphonic potential in the same genus for which Andrews claimed hearing by using a training method, but nobody has been able to substantiate Andrews's [2] results. Crocodiles and alligators probably hear; their anatomy would so indicate, and sound has an effect on the rate of breathing of these animals. Hearing ability in lizards is beyond question.

It remains to be proven that reptiles possess frequency-pitch discrimination, although one would be hard put to explain why those reptiles with a functionally advanced inner ear should be deficient in this sensory dimension.

Hearing in Birds.

The bird's lagena has reached the point of development where it is often referred to as the cochlea. Although it is long and uncoiled, its inner structure is much the same as the mammalian cochlea. The columella is still found at this level, but the tympanic membrane is located deep enough in the head to provide an external auditory meatus.

Birds appear to have a lower frequency range than man; the most generous estimate to date has placed the lower limit at 40 cycles and the upper limit at 14,000 cycles for parrots and crossbills. Frequency discrimination in these birds parallels that of man. Perhaps the best evidence, empirically, for a higher level of discrimination in birds is the ability to mimic. Parrots, mockingbirds, and parakeets are well known in this respect, although other birds are able to mimic both animate and inanimate sounds.

Naturalists have known for some time that the tremendous range of sound emitted by birds often has a communicative function. A renewed interest in instinctive behavior is bringing about studies which involve analysis of some of the sounds produced by birds.

At least one case is known where birds have been able to put their sound-producing and hearing ability to a noncommunicative purpose. This exception involves the oilbird of Venezuela. The species is known to exist in only one cavern, now protected by the government. It is of interest to scientists because it is nocturnal and performs its feats of navigation in total darkness by echolocation, as do bats. Griffin [21] analyzed the emitted click sounds with an electronic apparatus and found that each click had a duration of one- to two-thousandths of a second with a frequency of about seven thousand cycles. Since the wavelength is much longer than that of bats, the oilbird is probably a poorer navigator.

Hearing in Mammals

In all mammals the cochlea is well developed. The amount of spiraling may vary from a quarter turn to five turns, but the turns have no correlation with size, intelligence, or any other known factor. In terrestrial animals the connection between the middle ear and the eardrum is the three ossicles best known in man. The pinnae usually have some degree of mobility, but even where they have not, as in most humans, they still serve as reflectors of high frequencies.

Most of the experimentation on hearing in mammals has been confined to the common laboratory subjects—dogs, cats, and various rodents. Also in many cases the experimenter's control of the variables has been at a minimum and has been hampered by the fact that some animals have a superior hearing range.

The rodents have comparatively high upper limits. The white rat and the guinea pig place at about 40,000 cycles, while the mouse is thought to have an upper limit of 95,000 cycles. It has been known since the time of Galton that the dog is sensitive to ultrasonic sounds; it seems able to hear up to about 35,000 cycles. A recent study using modern electronic equipment set the cat's hearing from 62 to 60,000 cycles; above 4,000 cycles the sensitivity of the cat's ear is superior to man's, below 500 cycles it is inferior [35].

Comparative studies of intensity are practically nonexistent. One of the conclusions often drawn is that some animals, among them the dog, have keener hearing than man. It is not easy to see how this could be. The absolute threshold for man, 10^{-12} erg, is about as low as it could be without molecular action becoming audible. It is probable that additional vigilance on the part of the animal and its better sensitivity for high frequencies are responsible for the notion that the dog has more sensitive hearing than does man.

The frequency range of man is nothing exceptional, being from about 20 to 20,000 cycles. The chimpanzee, for example, has an upper limit of about 26,000 cycles.

The bat appears to hold honors for high-frequency reception. Galambos [15] studied the microphonic potential in bats and discovered that the effect persisted beyond the range of his equipment, which ended at about 98,000 cycles. Galambos and Griffin's [16] work on bats has accomplished much by way of explaining their space navigation. The principle is that of echolocation or sonic detection. The animal in flight emits ultrasonic sounds, generally between 30 and 70 kilocycles. Each cry lasts one- to two-thousandths of a second; the number of cries per unit time depends on whether the bat is at rest, flying in open space, approaching or leaving an object. The pharyngeal ventricles have become modified to act as resonators for the high-frequency emission. It is possible that the ears are screened from the larnyx so that the echo will not be confused with the emission when objects are close.

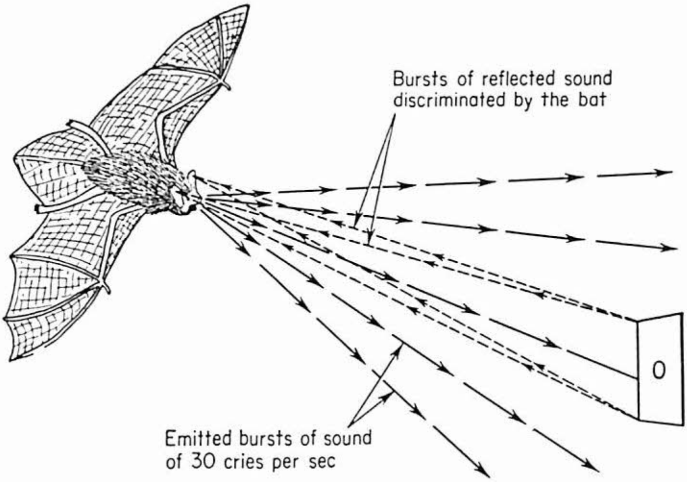
Bursts of reflected sound discriminated by the bat
O
Emitted bursts of sound of 30 cries per sec

FIG. 4-7. The principle of object localization and discrimination by the bat. [*From C. P. Stone (ed.), Comparative psychology. Englewood Cliffs, N.J.: Prentice-Hall, 1951, p. 324, fig. 5.*]

THE CHEMICAL SENSES

Chemical sensitivity may well be called a property of life itself. As a generalized or common chemical sense, it is found in protozoans and other low invertebrates, where no specific receptors can be postulated. Although higher phyla have developed special end organs for the detection of chemical effects, this common chemical sensitivity persists. It is the end organ, however, that has our interest here.

Köhler [26] has produced evidence of chemoreceptors for both distal and proximal reception in the head of free-living planaria. This distinction of chemoreceptors into functions is common in higher phyla; the separation becomes more clearly marked in the land-living vertebrates where the classification is that of smell and taste.

A general statement can be made that chemoreception on the whole has been more adequately studied in lower forms, that is, in invertebrates and low vertebrates, than it has in the higher animals. Particularly interesting are the results of experiments with insects, in which detailed information has been obtained. The sensitivity to sucrose is very marked in most of the insect forms when we compare the results with those found for man. Other studies, particularly those of Dethier [10], also offer conclusive evidence as to the usefulness of these organisms in determining some basic laws in chemoreception. In the study of fishes, much of the work done by Von Frisch, who also has carried out studies dealing with the chemoreception of bees, is perhaps the most important of the work done with vertebrates. It was Von Frisch [47] who found that the chemoreception in *Phoxinus laevis* is present in this species in such a way that it makes alarm responses in the presence of skin substances of its own and other species. The interpretation is that in a swarm of these animals, there will be a fright and escape response whenever skin is torn from one of the animals in the swarm, which presumably would be done by a predator fish.

Fish not only discriminate other species by their odor but actually are capable of discriminating individuals of their own species purely on the basis of smell.

Minnows have been used to study pollutants of lake stream water. By training techniques, it was shown that these fish could discriminate phenol compounds about twenty times more accurately than can man. The results are also important in research dealing with salmon homing and migration.

Chemoreception in amphibians has been studied relatively little, but Eibl-Eibesfeldt [11] found that the same phenomenon discovered by Von Frisch in *Phoxinus* was also present in the tadpoles of *Bufo vulgaris*. The substances released by the torn skin of these tadpoles caused other tadpoles of this species to take immediate flight to the bottom of the container. Snakes have been shown to follow the chemical traces of their prey, and turtles have been shown to have a well-developed sense of smell.

There is much confusion about the chemical sensitivity of birds. Engelmann [12], who has done most of the work dealing with taste capacities of birds, comes to the conclusion that although the sense of taste is in some respects rudimentary, it is present to some extent in all four taste qualities.

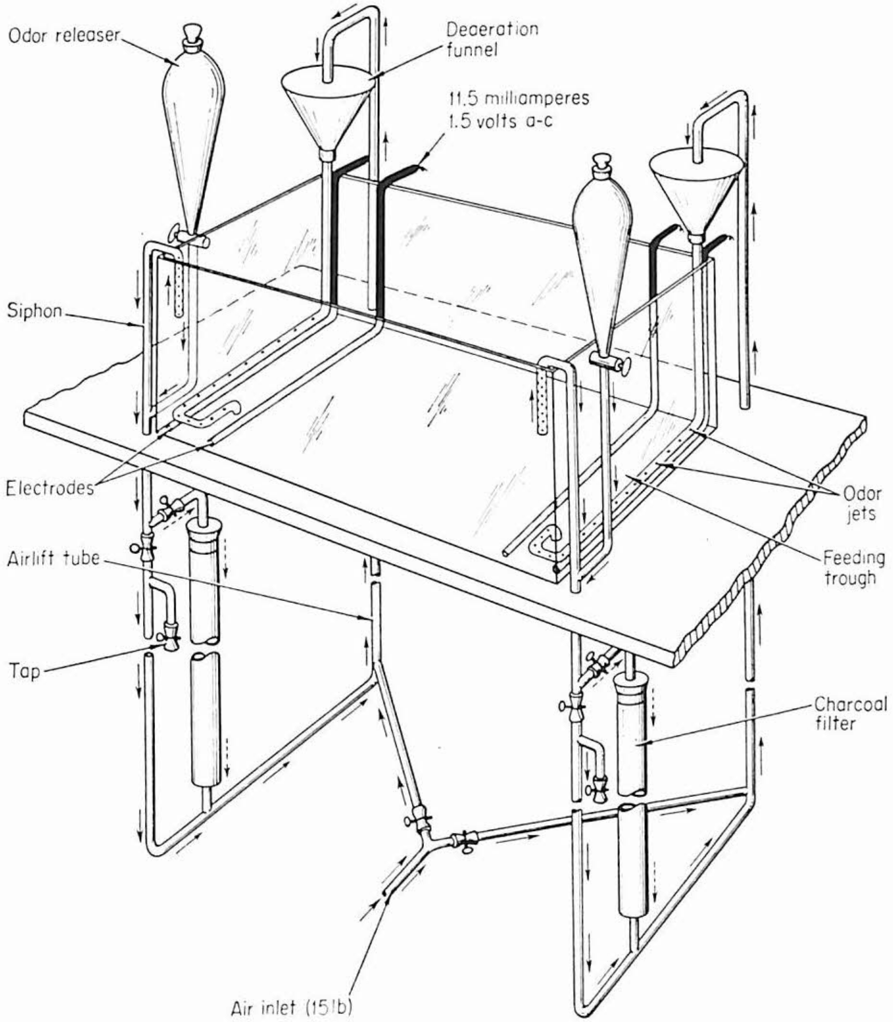

FIG. 4-8. The aquarium setup used by Hasler and Wisby to train and test fish in the comparative discrimination of odors. [*From C. P. Stone (ed.), Comparative psychology. Englewood Cliffs, N.J.: Prentice-Hall,* 1951, *p.* 326, *fig.* 6.]

Although it seems common knowledge that infrahuman mammals can taste and smell better than man, the experimental studies have not been particularly good. In most instances, conditioned-response techniques have been used, particularly to indicate sensitivities to smell in the dog.

Mainly as a result of the recording of action potentials, we have had an increase in the work dealing with chemoreception in mammals. Zottermann [53] determined that the cat has no specific receptor for the taste quality of sweetness. Pfaffmann [36], using the same animal, found three types of taste receptors: those which reacted only to sour, those which responded to salty and sour, and those which reacted to sour and bitter. Reactions to sweet were infrequent. Richter [40] determined the threshold for NaCl to be 0.055 per cent in the rat. The threshold for man is 0.016 per cent. After eliminating adrenals and as a result of the strong salt hunger of the rat, he found that the threshold went to the low value of 0.003 per cent.

Investigation of comparative sensitivity has been hindered both by lack of interest and the inability to find a comparative technique.

SUMMARY

This chapter began with a review of the four essential methods used in studies of sensory physiology and then briefly discussed some of the variables of the stimulus itself. Several words of caution may be said in connection with methods and variables. No written exposition can fully prepare the investigator in the use of methods; animals are notorious for their flagrant disregard of the tried and established; and a method which works perfectly well in one situation may not work at all in a slightly changed situation. By the same token, stimulus variables are sometimes lawful only in a statistical sense; the briefness of our summary compels us to consider the rule and not the exception.

If it seems at times that an undue amount of attention has been given to insects, it may be well to remember that above a certain level in the phylogenetic scale there has been little change in sensory processes. The insects represent a diverging scheme of things; in the main, a truly adequate review of comparative sensory physiology must therefore mention the different systems that developed in insects.

At the other extreme, we have made no attempt to give a detailed account, either anatomically or psychologically, of the human sense organs. Such detail may be found in practically any textbook of sensory physiology. As a matter of fact, most texts in this area do little but explain the human senses.

We have said what the present chapter is not. Now we shall say what it is, or what it is intended to be. It is intended as an introduction to the means whereby living creatures receive the stimuli that guide and direct them. The approach has been phyletic, and the aim was to give an informative but interesting glimpse of what is actually a large and complex field of study.

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CHAPTER 5

Biological Approach To Motivation

A frog in the mud at the bottom of the frozen pond or a lungfish in its mud cocoon in the hot African summer may appear to be completely inactive, but careful examination will demonstrate slow movement of the protoplasm, occasional heart beats, and slight movements of the blood. Some movement continues as long as protoplasm exists, and there is corresponding expenditure of energy.[*]

Observe simple marine life and you are immediately struck by the degree of energy expended in the apparent spontaneous movements—movements which appear unorganized and undirected but continual. Such activity, seemingly internally aroused, appears in the pink sea anemones, with their curling twisting tentacles; in the octopi, with their restless suction tubes moving over the surfaces of the water tank in which they have been placed. The tentacles, with their sensitive surfaces, move intermittently within the medium in which such organisms live and permit contact with the external, the geographic environment. Sometimes the contacts are followed by a specific pattern of responses, responses which permit ingestion of food for the animal, and the necessary fuel for the organism's motion is thus obtained. Again the contacts may evoke withdrawal behavior or other systematic patterns, though sometimes no systematic patterns appear, no selective direction is apparent in the activity stream.

Rises and falls in activity-level are characteristic of organisms throughout the phylogenetic scale. How intense, at times, is the motion of the young mammal, the puppy, the kitten, the child! The movement is continuous until sleep descends, though even then there are signs of alternating rise and fall in the breathing, the restless stirring, the whimpering. The boy, "Elsworth," in Figure 5-1 must at times sleep, but at the first glimmering of the dawn he is increasing his activity. Nor are all his motions merely gyrations: he may read or draw; he is often curious, sometimes afraid, frequently hungry, and his performance changes accordingly. "Elsworth" has goals; once he has attained some effect, he can symbolize

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[*] W. R. Breneman, *Animal form and function: an introduction to college zoology.* New York: Ginn, 1954. Pp. 6–7.

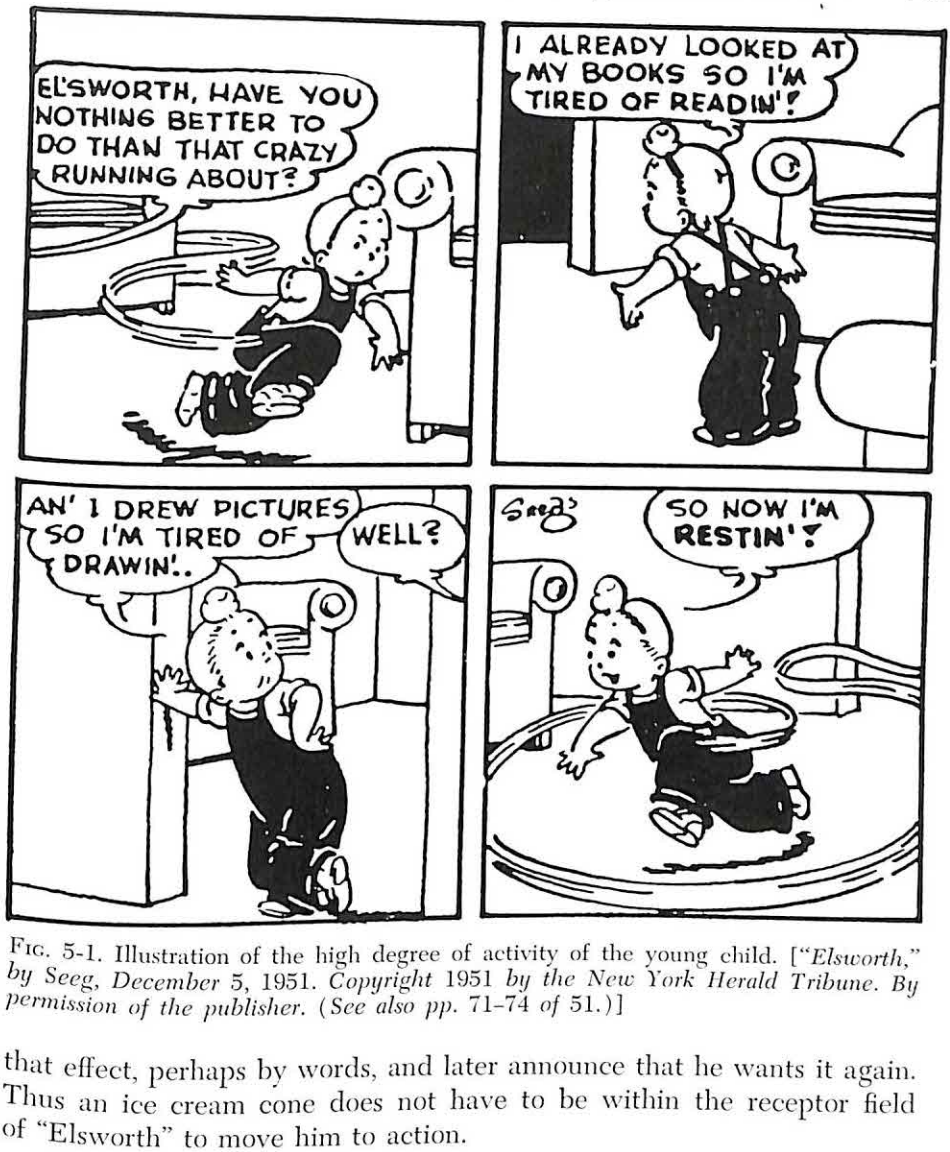
EL'SWORTH, HAVE YOU NOTHING BETTER TO DO THAN THAT CRAZY RUNNING ABOUT?
I ALREADY LOOKED AT MY BOOKS SO I'M TIRED OF READIN'!
AN' I DREW PICTURES SO I'M TIRED OF DRAWIN'..
WELL?
Seeg
SO NOW I'M RESTIN'!

FIG. 5-1. Illustration of the high degree of activity of the young child. [*"Elsworth," by Seeg, December* 5, 1951. *Copyright* 1951 *by the New York Herald Tribune. By permission of the publisher.* (*See also pp.* 71–74 *of* 51.)]

that effect, perhaps by words, and later announce that he wants it again. Thus an ice cream cone does not have to be within the receptor field of "Elsworth" to move him to action.

PROBLEMS OF MOTIVATION

The above examples illustrate that all organisms are inevitably active, but that there are rises and falls in the degree of activity. Being alive demands attachment of energy and constant expenditure of energy, but the amount released may be quite low, as in deep sleep, or quite high, as in flight from danger. One of the usually recognized problems of motivational psychology is to understand such *variations in activity-level.* Second, motivational psychology has also partly accepted as its responsibility the task of interpreting why *organisms are selective*, i.e., selective both in what they respond to as well as in how they respond. For example, any organism deprived of a necessary-for-life substance or object is likely to be sensitive to that of which he is deprived. If hungry, an organism is generally more selective of whatever is food for him. And the responses most likely to be evoked are relevant to his food need.

And a third general problem in motivational psychology is to study the *directions*, i.e., orientations toward ends, as observed in the activity streams of animals. For example, a spider weaves until a web is *completed*. Birds at certain seasons begin nesting and continue this activity until a nest of a particular pattern (form or shape) natural for their species is completed. The direction, in such cases, seems to be the completion of the web or the nest. Directions can also be learned, e.g., animals learn that goal objects, such as water for a thirsty animal, are located in certain places in the external field. Such learning apparently permits an orientation toward the learned goal. And in some unknown manner, the to-be-attained goal influences the animal so that there is a control over the natural variability. It should be noted that directional tendencies act upon the selecting mechanisms, even as many other factors do. Other problems of motivation, particularly those concerned with its role in learning, are considered in Chapters 6 and 13.

DRIVE AND DRIVES

Two concepts—drive and drives—are frequently used in motivational psychology. Drive is central excitation. Changes occur in central drive-level, as inferred from increases or decreases in the immediate vigor (intensity) of activity. When a man, for example, moves slowly, with little energy expenditure, "drags along," he has a low drive-level. And when he shows a lot of "push" in what he is attempting, when the intensity of his behavior increases, his drive-level goes up. Drive-level, tension-level, and excitation-level are used interchangeably. The variations in the level of drive are measured indirectly by recording scores of activity-level.

The locus of drive for the higher animals is probably in the hypothalmic or related neural areas. Both excitatory and inhibitory neural centers have been tentatively identified. Stellar's [76] physiological model for motivation, based on suggestions by Morgan [56] and Lashley [48], illustrates how varying central drive *may* be responsible for changes in behavior (Fig. 5-2).

There are various contributors to central drive, some energizing, some deenergizing. These are called *components of drive*, or simply *drives*. Drive is complex, with such interacting components as the drives of pain, novelty, noise, heat, cold, hunger, thirst, fear, etc. The particular drive components based on tissue disturbances are called need drives (primary drives). Though several drives may be active at one time, only one is dominant. Conflict may arise between drive components (drives), such as between fear and hunger. Drives may be learned (see Chap. 6).

Drives are motivational determinants, i.e., transient (temporary) variables in their influence on performance in one, or more than one, of three ways—activating, selecting, and/or directing. The transient property of drives is illustrated by the condition of hunger, which may be temporarily quite powerful in affecting the organism, but once sated, its influence disappears. Hunger, as other motivational determinants, may recur. The need drives, as thirst, pain, sex, and others, are characterized by their appearance, then disappearance, and reappearance. Emotions, frustrations, and similar affective drive states are also transient but recurring in their influence on performance. In contrast to the transient (motivational) states are the stable (nonmotivational) personality characteristics of individuals, such as physical structure, intelligence, traits of timidity or boldness, and, of course, habits of many kinds. Drives have different effects upon individuals according to their personality structure.

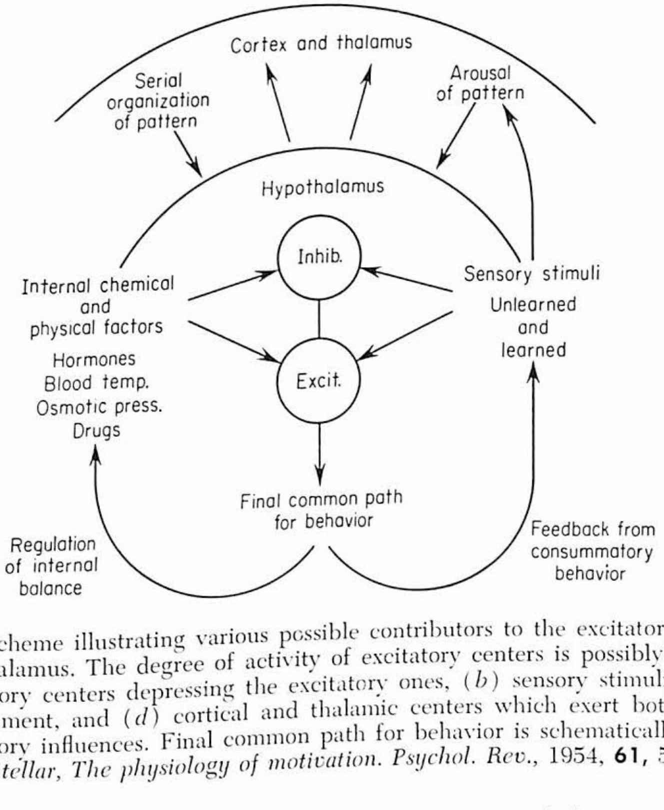
Cortex and thalamus
Serial organization of pattern
Arousal of pattern
Hypothalamus
Inhib.
Excit.
Internal chemical and physical factors
Hormones
Blood temp.
Osmotic press.
Drugs
Sensory stimuli
Unlearned and learned
Final common path for behavior
Regulation of internal balance
Feedback from consummatory behavior

FIG. 5-2. Scheme illustrating various possible contributors to the excitatory centers in the hypothalamus. The degree of activity of excitatory centers is possibly affected by (*a*) inhibitory centers depressing the excitatory ones, (*b*) sensory stimuli, (*c*) internal environment, and (*d*) cortical and thalamic centers which exert both excitatory and inhibitory influences. Final common path for behavior is schematically indicated. [*From E. Stellar, The physiology of motivation. Psychol. Rev.*, 1954, **61**, 5–22.]

For example, an intelligent man, with a lot of potential energy to release, strong in physical development, honest and kind, will be influenced accordingly by his transient drives. This same point may be illustrated with subhuman organisms. The personality of some rats may be characterized as hyperactive. Of other animals it may be said that they are hypoactive. (As indicated on pp. 334–335 active and inactive rats may be bred.) These are stable constitutional characteristics and are *not* motivational determinants. Of course, an individual rat who is generally hyperactive is accordingly influenced by his transient drives. When hungry, he probably exhibits more activity than a hypoactive individual. The interaction of the transient or motivational determinants and the stable personality characteristics is not well understood. It is not considered in this chapter except in a brief discussion of the interaction of one of the drives and a habit in affecting performance (see pp. 132–133).

Drives are *not* behavior patterns though often specific responses are correlated with their onset. For example, eating is a pattern of responses identifiably different from that of avoidance. With the more complex animals, learned behaviors are often associated with the different drives. (No attempt is made herein to link drives to "drive stimuli," to "demands," or to some other construct. Hull's [40] and Tolman's [81, 82] development of the topic of drives are considered in other sources.)

VARIATIONS IN ACTIVITY-LEVEL

The discussion below of variations in activity-level concerns the following: (*a*) methods of recording changes in activation (arousal) of organisms, (*b*) illustrative studies of antecedent conditions for drives and the correlated variations in activity-level, (*c*) recurring changes in activity-level, (*d*) effects of interacting combined drives. (Activity-level, activation-level, and degree of arousal are synonymous terms.)

Recording Changes in Activation-level

Measures of certain physiological and behavioral changes are indexes to the rise or fall in activity-level. The measures of *physiological* changes include scores on variations in basal metabolic rate, pulse rate, respiration rate, GSR (galvanic skin reflex), muscular tension, EEG (electroencephalogram), and others [22, 49]. Figure 5-3 illustrates a significant increase in muscular tension as the degree of motivation is raised. When human subjects performing in a tracking task are offered "large bonuses" and "threatened with strong electric shock," a significant increase in muscular tension is recorded (top line in Fig. 5-3).

Behavioral indexes to activity-level, more frequently employed with subhuman subjects, are obtained from measures of both *spontaneous* and

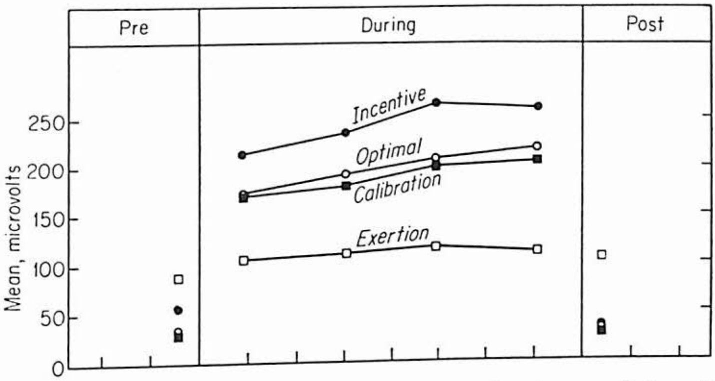

FIG. 5-3. Significant increase in muscular tension under increased incentives from money bonus and threat of electric shock (top line). "Optimal" refers to four best learning trials with small amount of money incentive. ("Calibration" and "exertion" established base lines.) [*From R. G. Stennett, The relationship of performance level to level of arousal. J. Exp. Psychol.,* 1957, **54,** 54–61.]

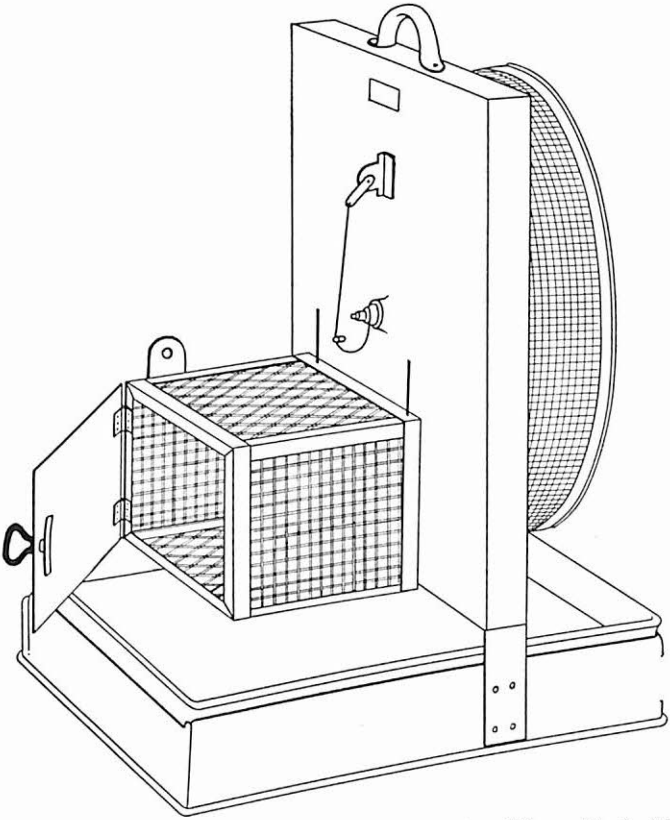

FIG. 5-4. Revolving drum for recording locomotor activity. [*From N. L. Munn, Handbook of psychological research on the rat: an introduction to animal psychology. New York: Houghton Mifflin,* 1950. *By permission of Geo. H. Wahmann Mfg. Co., Baltimore.*]

forced overt responses. The behavioral indexes are emphasized in this chapter. Spontaneous movements are recorded in situations where the organism may move but is not forced to respond. For example, when an animal is placed in an activity wheel (revolving drum) (Fig. 5-4), on a maze path (Fig. 5-5), or in a Skinner box (Fig. 5-6), he may or may not move. Any behavior is thus spontaneous. The activation is scored by the number of revolutions of the wheel, the speed of running, space covered in a maze, or the rate of the bar pressing in a Skinner-type apparatus. Subhuman animals are placed in such instruments and various motivational conditions are tested in order to determine changes in spontaneous behavior [75].

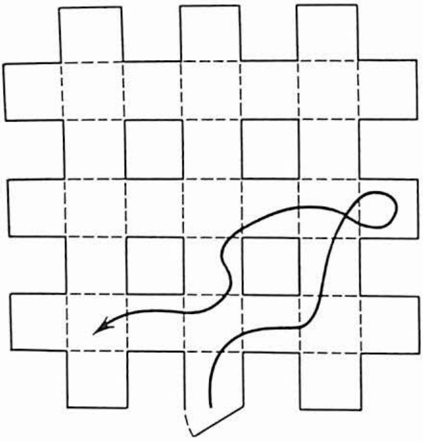

FIG. 5-5. Floor plan of Dashiell's open-alley maze for recording activity in a standard time period. The number of paths entered is the score. Heavy curve line is a sample record for a brief time period. [*From J. F. Dashiell, A quantitative demonstration of animal drive. J. Comp. Psych.,* 1925, **5**, 205–208. *By permission from J. F. Dashiell's Fundamentals of objective psychology. Copyright* 1937 *by Houghton Mifflin.*]

There is no hard and fast line between spontaneous and forced movements. The latter, however, are more predictable: e.g., when a nonaquatic animal is placed in a swimming tank, he must move in an appropriate swimming pattern or sink to the bottom and die. A painful stimulus also forces overt responses. The activation effect is recorded by noting increase or decrease in the latency, the amplitude, or in similar measures of the forced responses. Further changes

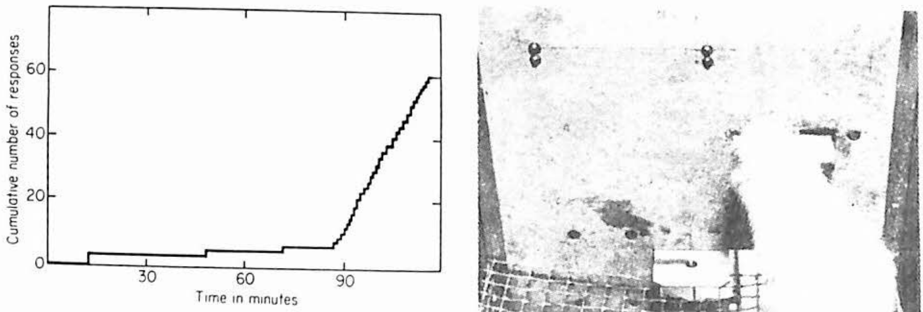

FIG. 5-6. A rat operating a food-delivery mechanism in a Skinner apparatus. Only one side of the usually enclosed box is shown. The graph illustrates the learning of a "beginner." Note that the first response did not occur until after 15 minutes had passed. (Other activity would not have been recorded.) [*From C. T. Morgan, Introduction to psychology. New York: McGraw-Hill,* 1956. *By permission from Clifford T. Morgan, Introduction to psychology. Copyright* 1956 *by McGraw-Hill.*]

in motivating conditions may be introduced, as decreased light or greater thirst, in order to determine any additional arousal effect on the forced behavior.

Records of activity-level variations, whether in spontaneous or forced movements, are necessarily *restricted*. One limitation is that the records are rarely made when complete freedom for responding is permitted, not even for spontaneous movements. Barriers to movement are frequently present during the recording operations. However, barriers are useful when systematically introduced to determine activity changes, as in frustration experiments when an animal under a goal influence is blocked. Or barriers, as a standard amount of electric shock, may be employed to determine how many times an organism under the influence of some need drive (thirst) will cross the shock barrier (to water). In the obstruction box (Fig. 5-7) devised by Moss [59] and used by others [86, 87, 88], the number of times a barrier is overcome in a fixed time interval (20 minutes) is an index to the level of motivation. Miller [54] also reports the use of quinine as a barrier to eating food in which the drug has been placed. Measurement of the degree of activation by the obstruction technique does not permit isolation of the different drive contributors. If the number of crossings of an electrified grid to food is recorded for a hungry animal, there is no way of isolating the degree of drive contributed by each of the following motivational determinants: hunger state, the anticipation of food, frustration arising from the barrier, and possibly exploratory tendency. Learning is also a possible but often an unknown contributing variable.

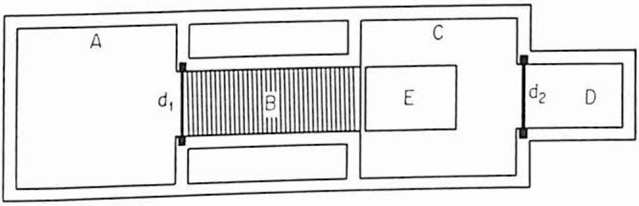

FIG. 5-7. Floor plan of an obstruction box permitting records of number of crossings of an electrified grid (*B*) from starting place (*A*) to the final goal box (*D*). The d_1 and d_2 are doors. *E* represents a release plate for door two. [*By permission from Carl J. Warden, Thomas N. Jenkins, and Lucien H. Warner, Comparative psychology (vertebrates). New York: Ronald,* 1936. *See C. J. Warden, Animal motivation. New York: Columbia Univer. Press,* 1931, *p.* 18, *fig.* 1.]

A second restriction is the impossibility of recording *all* activities. Theoretically, the effect of any motivational influence upon activity-level should be determined by records of variations in the intensity of *all* activities, physiological and behavioral. Most records, however, are limited to a narrow segment of the total activity-stream, often only *locomotor* behavior. One attempt to obtain a more representative sample of behavior is to modify the living cage of an animal so that many of the slight as well as the more gross behavioral adjustments are recorded. Such stabilimeter-type instruments, as well as the revolving wheels, permit records over several hours, even months of time. A stabilimeter recording instrument has been devised so that fine time units may be used, i.e., less than 0.5 second [61].

A series of studies [21, 78, 29] has attempted to measure the drive strength by means of recording rate of ingestion or number of copulatory responses, i.e., consummatory responses for need drives. These scores are not always related to other signs of drive change.

Drives and Variations in Activity-level

Arousal Changes under Need Drives. There are a variety of drive components called need drives (primary drives). They arise from such antecedent conditions as deficits of food, water, air, optimal temperature, rest, and activity. They also arise when there is interference with such activities as evacuation, micturition, and, at times, mating behavior. Painful stimulation is often listed as a source of primary need drive. Excesses of substances or of acts may also produce nonoptimal (nonhomeostatic) states of the internal environment.

All organisms have an internal environment and live in an external field. The animals who live in the sea have a different external world from those who live on the land. The internal environment is essentially the chemical medium supporting the neural system. This environment has greater similarities from species to species than the external field. Species may live in the sea or on the land, but their internal environments may be alike. "The vertebrate animals of today are the products of millions of years of evolution along widely divergent paths, and yet in many respects their internal environments are remarkably similar" [20, p. 209]. The continued existence of all warm-blooded animals demands the maintenance of constant states in respect to body temperature, pH of the blood (acidity-alkalinity balance), blood-sugar level, blood pressure, heart rate, salt and water balance, calcium and phosphorous balance, etc. Whenever there is a disturbance to these states, whether the *origin* of the disturbance is from the external or the internal environment (or both), the need drives arise. The organism then tends to set up regulatory (adaptive) activities which will prevent the disturbance from continuing. Motivational psychology is concerned whenever such regulatory activities depend upon the coordinating endocrine and neural systems.

Three of the need drives will serve to illustrate these sources of change in activity-level. The discussion of other need drives can be found in many texts [60, 91, 96].

Food Deficit. One of the most predictable changes in activation follows deprivation of all foods. In general, there is first a rise in the number and range of movements until physical exhaustion occurs. This relationship is reported for animals ranging from the protozoa to mammals [85]. Figure 5-8 indicates that the activity rise is a negatively accelerated increasing function of hours of food deprivation.* If a group of animals is deprived of food for a period longer than 48 hours, it is expected finally that *no* activity will be recorded, inasmuch as there will be no live subjects to test.

Such demonstrations of the activation changes under food deficits have been criticized as excessive, since it is claimed that extreme food deprivation rarely occurs among civilized men under normal living conditions. Certainly many social threats are more important in the motivation of the human species. By learning to store and distribute foods, man has shortened the time interval when he is without food, the necessary energy source. In the United States, overeating rather than food deprivation may be a more frequent source of nonoptimal internal conditions. However, the universality among diverse animal species of increased activity under hunger justifies the emphasis placed upon it. It represents a dependable source of variations in activity as is attested by its frequent use in learning studies. Of equal interest, though less frequently studied as an antecedent for a drive change, is overeating.

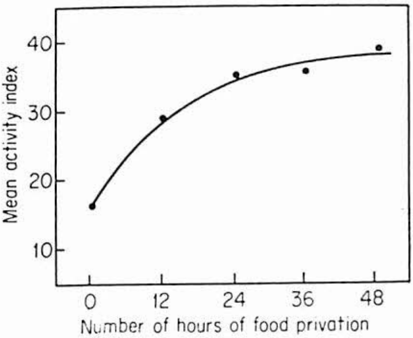

FIG. 5-8. The rise in activity of rats under increasing hours of food deprivation. [*From P. S. Siegel and M. Steinberg, Activity level as a function of hunger. J. Comp. Physiol. Psychol.,* 1955, **48,** 272–277.]

There are many *specific food needs.* These qualitative needs follow deprivations of specific substances, such as of protein, vitamins, etc. They arise with changes in food requirements due to maturation, aging, pregnancy, and lactation. Extremes of external temperature and other stress conditions may create special food needs. Structural insults to the body, as removal of the pancreas, the parathyroids, and the adrenals, are followed by needs for specific substances. The energizing influence of a specific food need is not as invariable as when the organism is deprived of all foods. Animals under a need for a specific substance *may* show a rise in activity-level, a decrease, or no change [65]. These specific needs, however, as well as general hunger, have motivational functions other than activation. (See p. 128 on selection.)

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* The curve does not show zero activity, even though the animals are not hungry. An organism always has some drive. As Campbell and Sheffield [13] point out, external stimulation is a factor affecting the degree of activity under hunger state.

Activation Changes under Disturbance to Water Balance. A state of water deficit leads to physiological and behavioral changes. A change in general activity under water deficit is reported for such subjects as dogs [30] and rats [32]. As with the nonhomeostatic states related to overeating, imbalance may originate from an *excess* as well as from a *deficit* of water. Adolph [2] states that frogs and earthworms suffer from excess, while mammals more frequently suffer from deficit of water. The origin of the disturbance to the water balance, and hence to a drive change, may be related to the external environment in which the organism lives. A frog in his usual moist atmosphere may absorb too much water; if kept from such an atmosphere, he then suffers from a water deficit. However, most of the systematic studies of the behavioral activating changes under condition of water imbalance have been made with mammals under water deficit.

Activation and Oxygen Need. Oxygen constitutes one of the major needed substances but deficits are infrequent. When an oxygen need arises, it leads only to minor changes in the behavioral scores of activity-level. If a man is placed in an artificial environment deficient in oxygen, he may at first have exaggerated feelings of well-being though physiologically he is suffering from the oxygen lack. Man, in his usual external world, seldom has any deficit of oxygen, and he has few regulatory mechanisms for preventing such a deficit from destroying him. A study [47] of the cockroach, honey bee, and mealworm suggests that their reactions under an oxygen need are also related to the degree that they encounter oxygen deficiency in their daily lives. The mealworm's normal habitat is in grain, where the circulation of air is extremely limited. This organism avoids entering the side of a T maze where there is 100 per cent carbon dioxide, but it makes chance responses between normal air and 50 per cent carbon dioxide. The mealworm either cannot discriminate the excess carbon dioxide or suffers no deleterious effect from the excess. Or possibly a need arises but has no effect on its behavior. Observations with the honey bee and the cockroach indicate that their reactions to the presence of an unusual degree of carbon dioxide are likewise related to the amount normally encountered in their habitat. A significant point is that organisms vary in regulatory mechanisms permitting adjustment to bodily threats. A tissue need may arise without any behavioral signs of activation. There are *deficit needs, as for certain vitamins not correlated with any signs of drive change*. And there are *drive changes which do not originate in deficit needs.* (See Chap. 6 for a discussion of exploration.)

Activation-level and Goals. The hungry animal may run in an activity wheel (Fig. 5-4) until his energy reserves are exhausted and death ensues. He apparently runs for "nothing," since he obtains no more food than if he had saved his energy. In fact, he dies more quickly under starvation because he is so active. Is this paradoxical behavior influenced by an anticipated goal of food? Having previously been fed when hungry, does he expect food? Though these questions cannot be answered directly, some observations cited below throw light on the activating function of goals. Goals are learned anticipations of to-be-attained effects, sometimes associated with approach behavior. (To-be-avoided effects are not goals; however, anticipation of success in avoidance may be a goal.)

Before reviewing briefly the observations demonstrating the relation of goals to activation-level, it is necessary to face a fundamental problem: how can a future goal affect the intensity level of the present performance? To imply that the "future" can influence the "present" is normally repugnant to the scientists. However, when it is said that a future goal influences present activity-level, it is assumed that there is a learned substitute (a symbol) of the to-be-attained effect. Man may use words to symbolize a goal, e.g., he may say that he wants to "buy a farm." Such symbols, in some unknown way, influence the degree of released energy channeled into behaviors usually appropriate in reaching the goal. Probably man also uses nonverbal symbols such as some of the subhuman organisms may employ. Tolman [82] hypothesizes that organisms may acquire central expectancies of "what-leads-to-what." Hull [40] suggests that fractional anticipatory goal responses (acting as stimuli) represent to-be-attained effects, and may contribute to drive-level.

Various animal forms are energized according to what they learn are the end effects of acts. Chickens move faster through a maze when they have an opportunity to learn that several grains of rice (instead of one grain) are at the end of the path [31]. The inciting influence of goals upon the performance level of rats has been demonstrated in other devices for recording activity-level [28]. (Contradictory results are also reported [73].) Chimpanzees "work harder" to pull to their cages a visible piece of banana when it is increased in size [27]. (These primates were required to pull the food a distance of 18 feet, and the resistance was varied by the use of braking devices or by attached weights.) Chimpanzees discriminate among tokens according to their exchange value for different amounts of reward [93].

A terminal goal may vary in many ways. Food, for example, may vary in size, weight, nutritional value, taste, texture, number of consummatory responses required to ingest, color, shape, and its container. The most frequently demonstrated relation between characteristics of food goals and their inciting effects is between variations of quantity and activation. Quantity, however, is not a simple attribute: it may be changed by increasing or decreasing the number of food pieces, by varying the time of contact with the food, and even by reducing size but increasing nutritional value. Each characteristic or combination of characteristics of terminal goals requires independent investigation in order to determine its particular activating contribution. (Various controls are obviously necessary for comparisons among studies, such as degree of hunger, the activating measure used, and the number of times the goal is attained.)

Wolfe and Kaplon [94] found that the number of "pieces" of food rather than the actual amount was significant in inciting their subjects (chickens). One grain of corn, cut into four parts, contributed more to central drive. Why? Did the increased number of anticipatory goal responses determine the greater energizing effect of the four pieces of food? Whatever the answer to this question, it can be said that characteristics of the goal, including the number of separate parts, are related to the degree of energy released into approach behavior.

Preferences for goals influence their drive effect; e.g., sucrose, a highly acceptable substance to animals, has a greater inciting value than a goal of lesser preference. Activation-level (speed of approach) changes as the amount of sucrose at the goal place is increased. "The speed at which rats approach a sugar solution, after brief daily tastes of it, is an increasing monotonic function of the concentration" [100, p. 305]. The effect of the varying concentrations of sugar is observed even when the subjects are neither hungry, thirsty, nor depleted in any known way. In another study [42] both preferred flavor and size of food pellets influenced the activity-level, as indicated by the rate of bar pressing in a Skinner-type apparatus. The rates of performance, presented in Figure 5-9, under the different combinations of size and flavor are in the same order as found on independent preference tests. (The pellets used were small, medium, or large, and saccharin flavor, basic diet, or citric flavor.)

When there is a change from a preferred goal to one of lesser acceptability, activity-level is decreased, apparently by the contrast between the previously attained and the new goal. If the shift is to a goal of higher preference, there is a rise in activation. In their daily lives, men report being elated or depressed according to the contrast of their immediate pay to previous wages. When they obtain more than usual, they are elated; when less, they report being depressed or, in some cases, angry. This same contrast effect occurs in subhuman animals, if behavioral signs of activity-level variations may be so interpreted. Chimpanzees show signs of disappointment when the usual peanut or grape does not follow a response which they have practiced. Or if the reward object, which they perceive is placed in a goal box, is shifted to a

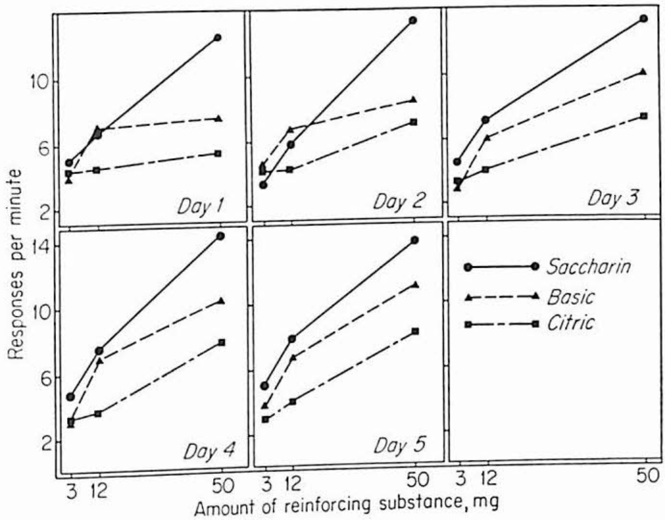

FIG. 5-9. The more preferred the flavor and the greater the size of food reward the more the activity. [*From P. J. Hutt, Rate of bar pressing as a function of quality and quantity of food reward. J. Comp. Physiol. Psychol.*, 1954, **47**, 235–239.]

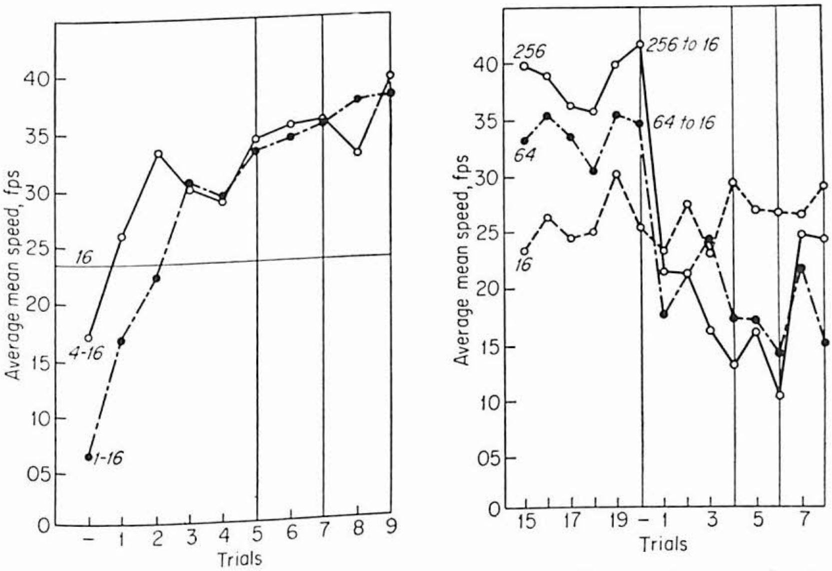

FIG. 5-10. A change in size of food reward (increase or decrease) is correlated with a change in activity-level. On the left the increase is from a small amount of food to sixteen pellets. The animals run faster than the controls also rewarded with sixteen pellets. On the right side of the graph, the shift illustrated is to sixteen food pellets from a greater number. The speed of the animals falls below the usual 16-unit level. [*From Hull* (41). *As adapted from Crespi* (16). *By permission from Clark L. Hull, A behavior system. Copyright* 1952 *by Yale Univer. Press, New Haven.*]

reward of lesser preference, they behaviorally exhibit disappointment or there may be observed a "chimpanzee rage." The effect of shifting a goal up or down a scale of preference also influences the performance level of infraprimates [16, 101]. As seen in Figure 5-10, the change in quantity of food to a lesser amount than previously received depresses the activity of rats even below that normally observed under the new goal. And when the shift is to a larger quantity than found on many previous trials, the animals increase in speed. They are said to be elated, since their rate of movement is even greater than the rate of the control animals.

Man is probably the only animal who is affected by a comparison of his goals with those of other individuals. He may raise his own goals perhaps trying to "keep up with the Joneses." A man may also contrast his "pay" with that attained by his coworkers. If others are obtaining $100 for a standard job, then $50 seems like "small potatoes" to him. Man's drive is affected by these contrasts. He may become depressed, angry, elated, even fearful by such contrasts and be accordingly affected in his drive. As noted in the next section on frustration, the emotions are significant contributors to the immediate motivational level.

An important *question:* are the different activating effects of shifts in goals the result of learning rather than of motivation? In the studies cited above the larger goals are correlated with an improvement in speed of running. Are the animals, given an increased amount of food, learning in a superior fashion, *or* are they performing at a higher level because their drive is greater? Reynolds [67, 68] and others [95] suggest that such variations in performance are motivational in origin. It is assumed that the learning strength is *not* affected by the increase in the reward but that the drive-level goes up. The best support for this hypothesis is the finding that shifts in the size of reward suddenly change performance. Learning is not usually abrupt, except in the case of insights. It should be remembered, however, that learning is always a possible influence on the level of activation. Several attempts have been made to isolate the contributions to performance level of learning and of drive. No conclusions can be drawn, save that both are significant.

Activation-level and Frustration. Frustration, that organismic state which arises following interference, contributes to drive-level as inferred, of course, from changes in amount of activity. After interference there may be a rise in the vigor of all responses, and intensification of any ongoing act. More probably the increased release of energy is observed in the vigor of responses which might overcome the interference.* Finch

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* Interference (interruption) is the general antecedent condition for frustration. Brown and Farber point to a number of different kinds of manipulable conditions used in arousing frustration: "(*a*) the introduction of partial or complete physical

[26], for example, reports that chimpanzees press the operating handle of a water spigot more frequently and with increasing vigor when it fails to deliver water. Rats increase their running speed after the frustration of finding a goal box empty; they run faster to a second box where in the past they always found a pellet of food [6].

Intensification of activity under frustration is not invariable. Many factors are involved: the nature of the interference, degree of strength of the original source of the interrupted activity, the goal of the interrupted act, the expected outcome of an attack on the frustrating agent, the length of time that the frustration continues, and probably the success (immediate, or in the past) of attempting to overcome the frustration. Many of these and other variables have been investigated. After reviewing some of the evidence, Brown and Farber [12] conclude that frustration contributes to drive.

Observations of human as well as subhuman subjects under frustration raise another problem in motivation: *what are the best indexes that drive has changed?* Behavioral indications of drive change under frustration may be peculiarly confusing, since inner tension may rise when behavioral signs of drive change are absent. Or perhaps there is even a decrease in overt activity under frustration. When the animal is behaviorally quieted under interference, physiological measures of tension may indicate that inner excitation is actually heightened. This tension may even increase to the point of upsetting the homeostasis of the organism.

The above is necessarily an incomplete discussion of drive variations under interference. In the next section an even wider class of energizing and deenergizing motivational determinants is considered, namely, stimulation.

Activation-level and Stimulation. Organisms are sensitive to many sources of energy change. Consequently it may be said that organisms basically vary in what will activate them. This same point is sometimes phrased as follows: organisms are continuously motivated (activated) because they are constantly being affected by stimulation, though, of course, in varying degree. In other words, there is always stimulation, sometimes a lot, sometimes very little. Even if all internal sources of excitation were reduced, which never happens, there would still be some external excitatory influences. Because of this constant bombardment from stimulation, this continuous contribution to central excitation-level, organisms have adjustive mechanisms for preventing overexcitation, i.e.,

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barriers; (*b*) the introduction of delay periods between the initiation and completion of a response sequence; (*c*) the omission or reduction of a customary reward on one or more trials; and (*d*) variations in the organism's condition, environment, or training leading to the evocation of a response tendency that is incompatible with an ongoing one" [12, p. 481].

nonoptimal drive. Sensory adaptation is apparently one way of ruling out too much stimulation. Sleep seems to work in the same way. On the other side of the coin, it is important to note that too little stimulation is reported as disturbing [38].

Stimulation is broadly defined in the above. It is assumed to be any determinant which raises or lowers central excitation. It is not assumed that those particular specialized organs called receptors are the only mechanisms for increasing or decreasing central excitation. As seen in Figure 5-2, chemical and physical factors of the internal environment may influence the inhibitory or excitatory neural centers of the hypothalmus. It is also possible that there is drive of the hypothalmus itself.

Observations of stimulation from the *external* field permit a few tentative conclusions in regard to their effects on arousal:

1. The greater the number of external stimulating agents, the greater the observed changes in activity-level, provided they are all energizing sources. Morgan [58] found that human subjects working on a task similar to typewriting increase the force of their finger movements when stimulated by bells, plus buzzers, plus phonograph records. As noise increases, there is also a greater oxygen consumption [35].

2. The dynamic effects of external-in-origin stimulating events may combine with those from need drives. The resulting change in activation varies according to the particular combination of stimuli and internal needs. For example, "bright lights" and "loud sounds" combine to raise drive-level *when* the individual is, in addition, energized by hunger. If the organism has a need for rest, any external stimulating events probably would raise central drive-level, though not to the same extent as when he is rested. Fatigue *may* cancel the dynamic effect of noise. As noted above, adaptation to stimulation also rapidly reduces its influence.

3. Stimuli from the external world most frequently function as energizers, though the human organism may be relaxed by soft music, warm water, and possibly certain colors.

4. All stimuli are not irritants, in the sense of being disturbing to the organism. Even those which raise the activity-level are not necessarily irritating.

5. Many stimuli may acquire, by conditioning, additional drive.

6. Stimulation from the social field often adds to the drive-level. Allee [3] states that fish swim more rapidly when together than when alone. The response thresholds of certain instinctive patterns are lowered under the exciting effect of other members of the same species. The instinctive mating pattern is more easily aroused when the animal is stimulated by a receptive partner. The complex social field of man has its own drive contributions, e.g., there are the exciting stimuli of the restless movements ("milling") of a crowd before it turns to mob action.

Finally, it should be noted that the dynamic effects of stimulation from external sources are in part dependent upon the "total situation." A sound source of great volume may have very little or no energizing effect, while a whispered warning may be followed by a burst of activity.

Recurring Changes in Activity-level

In any organism's stream of activity there are recurring variations. There may be a rise, then a fall, in the intensity of activity. Or the change may be identified by the appearance, then disappearance, of some inherent response pattern (eating, sleeping) or of some reappearing learned pattern (dating every Saturday night). Of particular concern in this section are the *recurrences in intensity* of activity. They may be periodic or aperiodic. Their origins are both internal and external to the organism.

Of interest are the recurring secretions of the endocrine glands with resulting variations in hormonal content of the blood stream and consequent cycles in activity. The endocrine glands and their specific hormones are described in various texts [8, 91]. The chemistry of the endocrines is said to be remarkably constant throughout the phylogenetic scale, e.g., both the chicken and the chimpanzee become aggressive under large doses of testosterone (the male hormone). (It has been questioned whether hormonal changes should be called origins of drives [37]. They are, however, accepted herein as sources of drive components.)

The discussion below first presents illustrations of cycles in the activity stream: diurnal (including sleep rhythms), seasonal, sexual, and life cycles. Then there is a brief consideration of the interacting influences of three general origins of such cycles: (*a*) recurring tissue variations, (*b*) reappearing external events as light-dark, and (*c*) built-in rhythms.*

Diurnal Cycles. The diurnal rhythm designates the 24-hour cycle of general activity changes which recur with day and night. Nocturnal, auroral, or vesperal designate general rhythms when the marked rise in activity centers around the night, morning, or evening hours. Rats, as illustrated in the diagram below, are nocturnal animals. Long-term cyclical changes (infrequent shifts from high to low degree of amount of movement) may be imposed upon short-term periodicities. The schematic presentation in Figure 5-11 is the overlapping of the diurnal and the 2-hour feeding cycle of rats.

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* Activity cycles are under the influence of nonmotivational determinants. If the health of the individual is "poor," if little food has been ingested for some time, or if for some other reason there has been an exhaustion of the potential energy available for release into activity, the cyclical *pattern* is affected. For example, he would be inactive longer than he would be active, and high "peaks" would be absent.

Sleep Rhythms. In whatever manner sleep is described and to whatever antecedent conditions it is traced, there is no doubt that it represents a cycle in the activation of organisms. Whether the changes are reported as a shift in the EEG pattern, in cognitive changes, in physiological variation, or in the decline of overt action and a decrease of general alertness, sleep comes and goes. The primitive sleep rhythm, as reported by Kleitman [46] for the human infant, changes with maturation and is subject to conditioning. The antecedent conditions necessary to bring the low level of activation observed in sleep are not known, though deprivation from sleep is inevitably followed by a return to it.

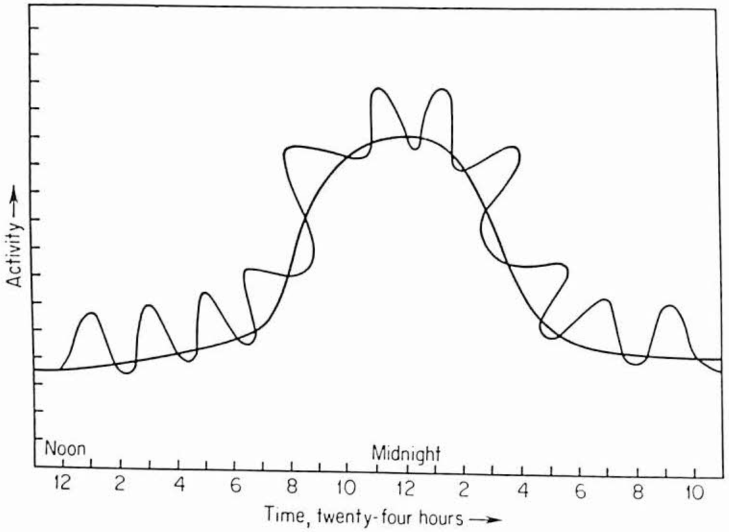

FIG. 5-11. Schematic representation of overlapping of diurnal activity cycle and approximately a 2-hour feeding rhythm in rats. (Irregularity in the appearance of such cycles is expected. Note also that if animals are fed only once per 24 hours, the above cycles will be affected.)

Seasonal Cycles of Activity. A marked change in the level of activity of some animals is correlated with the seasons, e.g., hibernation, migration, and mating. Recurring external influences, terrestrial or cosmic, are synchronized with the cyclical activity of internal tissues and correlated seasonal behavior changes. For example, changes in external events, as temperature in the spring, bring a change in the diurnal activity pattern of sparrows [25]. This shift in the daily rhythm is attributed to a gradually improving metabolic state correlated with increase in activity of the anterior pituitary. An overall increase in activity-level is observed with a greater rise at night. Seasonal variations are also reported in the physiological measures of adolescent boys and girls; BMR and pulse rate fell during the spring months and rose during autumn [53].

Life Cycles. Life cycles may be described in terms of changing sexual responsiveness. Thus Schneirla writes of social insects: "The individuals of many animal forms produce their gametes at fairly regular intervals in a recognizable rhythm; social insects characteristically produce sexual forms seasonally. The life cycle of birth, development, and senescence in an individual organism is paralleled in social insects by colony foundation, expansion, and degeneration" [72, p. 92]. In the life cycle of a normal individual of the human species, there is a single long period in which mating activity may occur, beginning with the maturation of the gonads at puberty. In some way, the anterior pituitary gland is stimulated to activity at this time in the life cycle. It begins to elaborate and secrete large quantities of gonadotropic hormones. In the male these hormones "stimulate sperm making and the secretions of androgens, which are the gonadal hormones." Similar changes occur in the female. Mating behavior starts. This period of sexual activity continues until it ends in sexual "senility," rather suddenly in the female, more gradually in the male. The sexual activity and drive decrease as the gonads regress.

The life cycles are found surprisingly similar in successive generations of simple organisms. And at the top of the phylogenetic scale, man also lives as those before him have. In spite of cultural changes through centuries and variations from one culture to another within the same period, all men move through similar life stages—from the "mewling and puking" infant to "sans teeth, sans eyes, sans taste, sans everything."

Origins of Cycles in Activation. The typical cycles described above are the resultant of a variety of interacting factors. Three general origins are (*a*) intrinsic (built-in) rhythms of organismic processes, (*b*) extrinsic (external) recurring events as day-night cycle, (*c*) recurring internal tissue changes from bodily deficits and excesses or from cyclical endocrine secretions.

The built-in rhythms of organismic processes are illustrated in the observations of Coghill and Watkins [15]. They report a pronounced cycle of responsiveness to light touch in their investigation of the larvae of the *Amblystoma.* There is first a rise in sensitivity to tactile stimulation, then a fall, then follows a rise again in responsiveness. The fluctuation continues indefinitely. The investigators are convinced that the cause of the cycle lies in the sensory receptors. Fatigue, as ordinarily understood, is said not to be involved. Beach [8], reporting the study, writes that the phenomena described may represent a general primitive type of periodicity in organismic activity, which may underlie more complex forms of behavior, such as the running cycles of the rat. Human infants are likewise characterized by a rise and fall in activity-level, with the change occurring approximately every fifty to sixty minutes. This short-term cycle is discernible whether the infant is asleep or awake. Kleitman

[46] suggests three possible interpretations of this intrinsic rhythm: it may be the resultant of metabolic variation or due to a pacemaker discharge. Possibly it is a fatigue-recovery phenomenon. Like the cardiac and respiratory physiological cycles, it tends to lengthen with age.

An important point in understanding cycles of organismic activity is that a built-in predisposition for a cyclical variation *may* not function unless there are the essential external driving events to which the changes must be geared [11]. For example, the adult Mayfly nymph normally exhibits a daily rise and fall in activity, but this rhythm is absent in insects bred from eggs kept in continuous light. A single exposure, however, to the light-dark changes of the 24-hour period is sufficient to establish the normal daily rhythm of activity. And once evoked, it continues independently of further changes in the external lighting [34]. In some unknown manner, the rhythm becomes deeply ingrained in the developing organism and later influences the behavior of the adult insects.

Cycles of activation represent an important aspect of motivation. Cycles in feelings, recurring moods, and similar affective periodic variations also need development in motivational psychology. They are not independent of recurring external events but are probably most closely tied to secretions of the endocrine glands. The interaction of the variety of factors operating upon cycles is illustrated by studies of the influence of the secretions of the pituitary gland. The *internal* secretions of this endocrine are probably *intrinsically* cyclical, though also affected by such recurring events in the *external* field as the length of daylight, temperature, rainfall, food supply, and even sounds [8]. Based on a variety of antecedent conditions, recurring drives arise in the flux of central excitation. The interacting and recurring drive components along with the intrinsic rhythms are responsible for cycles in activation level. In the next section, there is a further attempt to throw light upon the *interaction of drives.*

Interaction of Drives

Combinations of energizing and deenergizing drives are not unusual. In many life situations a given habit is motivated by more than one drive. For example, "the habit of working for money has been learned in response to a number of drives which were present either simultaneously or successively. In order to better understand motivation in many social and clinical situations we need to know more about how different drives combine" [64, p. 1]. A man is often concomitantly hungry, thirsty, sexually primed, irritated by painful stimuli, anxious about the outcome of an ongoing task, and possibly depressed by the anticipation of a lower reward than previously attained for completing the task in which he is engaged. And there may also be within his external environment many energizing stimulating sources, as irregular sound vibrations with sufficient volume so that he cannot easily adapt to the noise. And there may be deenergizing extrinsic agents acting upon him. The temperature of the external field may be so extreme that he is unable to proceed at his usual speed. Fatigue, boredom, and need for sleep may be depressing him. In addition, there are the possible influences of cycles of activity, some inherent, some acquired, some dependent on recurring external stimuli, all interacting, overlapping, perhaps summating, or again interfering with each other. The final outcome is difficult to predict.

Illustrative Studies. Hall's [33] study illustrates the additive effect of several drive components. The subjects (male rats) in revolving drums

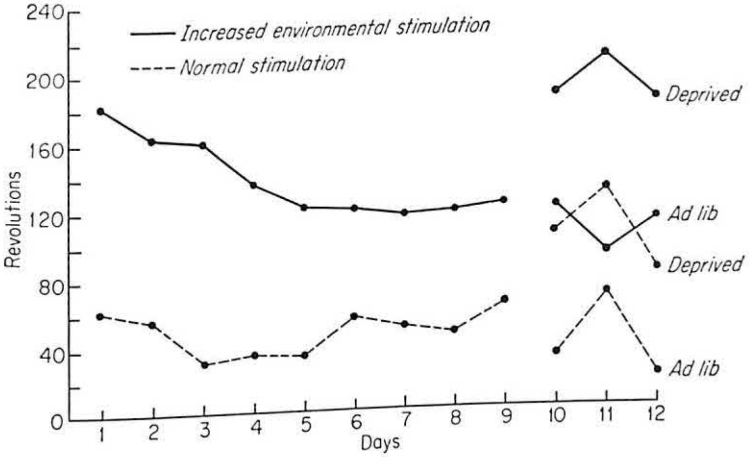

Fig. 5-12. Greater environmental stimulation plus food deprivation increases the activity-level as measured by revolutions of revolving drum. [*From J. F. Hall, Activity as a function of restricted drinking schedule. J. Comp. Physiol. Psychol.*, 1955, **48,** 265–266.]

are first under the influence of a minimum of external stimulation, i.e., in darkness, with a uniform temperature, and with little auditory stimulation, save the sound of the moving wheels. Moreover, the animals are neither hungry nor thirsty. In Figure 5-12, the line marked "normal stimulation" represents the activity-level under these motivational conditions. The activity-level rises when the external stimulation is increased (flashing lights and "considerable increase in auditory stimulation"). Following these changes in the external field, the animals are also deprived of food, and there is a further additive effect on the drive-level. Other observations support the implication from the above study; there is an interaction of concomitant drive components in their influence on performance level. Sometimes there is a subtractive, or, also observed, an additive effect [See 97, pp. 146 to 148]. Moderate thirst will support the learning and performance of an instrumental act to obtain food [44]. The strength of a response learned under hunger improves as there is an increasing degree of thirst introduced during tests of experimental extinction [89]. And, as indicated in the next chapter, a need drive increases exploratory activity [1]. Nonhungry subjects (rats) also run faster to food under a learned drive when they are in addition made thirsty [92].

A need drive may combine with a learned drive (anxiety) and intensify an avoidance response [4]. On the other hand, when an approach behavior to food was learned under hunger, the adding of the anxiety drive did not support the habit. A tone when followed by electric shock and presumably setting up anxiety *depressed* the rate of lever-pressing response to get food [24]. The animals seemed to "freeze" when the tone sounded.

Woodworth [96] questions whether anxiety could ever intensify a positive behavior. He asks whether there could ever be a redirection of anxiety drive into positive (approach) behavior. There is not sufficient evidence to attempt an answer to this controversial question. Some studies [5, 83] suggest that anxiety may, sometimes at least, support positive behavior such as approaching food or water and exhibiting consummatory responses. Ullman [83] reports for rats that the emotionality generated from continuous irritation (electric shock) was correlated with increased eating. He suggested that eating became a generalized tension-reducing habit similar to the compulsive habits of humans said to reduce their anxieties.

From the above illustrative studies, it can be concluded that combined drives influence the overall excitation-level as measured by various scores of activity-level. In general, the greater the number of energizing drive sources the greater the intensity of whatever responses are evoked. *What particular responses are evoked, however, is an important and a different motivational problem.* In one study [90], a specific response was learned under hunger. However, when the animals were food satiated, this specific response was also evoked under an irrelevant water-avoidance drive, though preliminary study indicated the irrelevant drives of electric shock or noise only brought forth crouching responses or highly disturbed behavior. The particular channel of motor expression of drive is influenced by the interaction of whatever are the dominant drive components. Before considering this point any further, a few statements are added concerning *physiological* interaction under combined need drives.

Studies of animals under both food and water deprivation suggest that their behavior is in part the resultant of a physiological interaction within the internal environment. The tissues of the body are changed when the animal is deprived of nutriments; and even if there is no deficit of water, an organism subjected to food deprivation limits himself in his intake of water [84]. It is *as if* the change in the internal tissues following food deficit decreases in some way the normal need for water. Gregerson [30], using dogs undergoing fasting, found that they reduced their intake of water during a 24-hour period to around one-fourth of their normal intake. Within 2 to 5 hours after feeding, the animals would then usually drink all the water that they would take in the 24-hour period, regardless of the time that the food was presented. Gregerson suggested that the concentration of water drinking after eating was due to the withdrawal of water from the body for the secretions of digestive juices. It is thus possible that the self-reduction of water intake when the animals are not eating is due to a lessened need for water. Animals will also reduce their eating when under water deficit, even though food is present in the external field [84]. In this case the dehydration under the water deficit possibly prevents normal secretion of digestive juices, and hence the animal has a lessened need drive for food. It can, at least, be concluded that studies of drives, particularly those based on tissue disturbances, must face the problem of possible physiological interaction.

Combined Drives Associated with Incompatible Response Systems. For every drive component, whether it is pain, hunger, fear, noise, novelty, anticipated goal, frustration, or others, there may be an associated appropriate response pattern—either a quite general pattern, as "avoidance" or "approach," or perhaps a quite specific one, as "pushing on a lever." Drives may be combined but their associated responses may be incompatible. Assume, for example, an animal is both hungry and fearful at a feeding place. Will he run or will he approach and eat? "Eating food" and "running away from food" are obviously incompatible. The question immediately occurs: what determines the final outcome? (There are other influences upon the final outcome, but we are here concerned only with drives.) The strongest drive component may win, and behavior is thus affected. If the animal is more fearful than hungry, he runs away. His behavior may indicate that the two drives are alternately in control of the final motor channel: i.e., he runs away, then stops, and starts an approach behavior to the food. When one of the drives dominates in a conflict because of its strength, the others are called extra, or irrelevant. They may support, or subtract from the vigor of the performance related to the dominant one.

The isolation, however, of the variables that affect the strength of any drive component has been difficult. To some degree the time of deprivation (up to a certain point) of some necessary substance or act is related to the strength of a need drive. And the degree of drive from pain, noise, light, and similar sensory inputs is related to the physical characteristics of the stimulating sources; e.g., pain usually increases as the amount of electric shock is increased. The best indication of the strength of any driving agent is, however, its effect on behavior. Nor is strength alone the sole determinant of whether a drive component is dominant in any conflict over the final motor pathways. A weak drive may possibly be behaviorally expressed *if* it is associated with a *well-practiced* response system. Any further consideration of the interaction of motivational and nonmotivational determinants on the performance of animals would take us into areas of investigation which cannot be developed in this chapter. In the next section, "Variations in Selection," the problem of the influence of drives on the evocation of responses is briefly reconsidered.

What determines variations in *activation* is the first motivational topic developed in this chapter. We now turn to the second, which concerns the *selective* role of drives as demonstrated in (*a*) the organism's structuring of the external world and (*b*) his selective evocation of particular response systems.

VARIATIONS IN SELECTIONS

Significant facets of motivation are revealed by the records of the selections of organisms. Men are said to select their foods, their vocations, and their wives, though it is likely that in the last case the selections are by the women. Nor are selective factors absent in the lower organisms. The "time since the last meal" of the hydra determines its response to the food stimulus [39, p. 147]. In the discussion below the interest is no longer in the intensity of the responses; no attention is paid to the latency, the rate of movement, and the amplitude of the responses. Whether the selections are slow or fast is of no significance.

Selections occur among potential stimuli in the external field and among potential responses. Assume that a child is presented with two potential stimulating objects, perhaps a toy and an orange. The mere fact that these two objects are in the external world does not necessitate that they are stimulating agents to the child. However, if both excite the receptors, presumably one will become the *figure* against the *ground* of the total field. In other words, selection is inevitable in perceiving. There is a constant filtering of potential stimulations provided by the external environment. Among the variables affecting this filtering are need drives. Beach reports [9] in *Body Chemistry and Perception* some of the correlations found between reported perceptions by human subjects and varying conditions of the internal environment. Both general and specific needs, for example, are reflected into the *perceptual structures* of children [23, 71] and adults [52]. Such studies suggest that if the child of the above illustration had a specific hunger for an orange, it would probably be the *figure* in his perceptual organization. In other words, the orange would stand out in his field.

Response selecting is likewise inevitable, provided, of course, that there is some behavior. In the particular illustration of a child focused upon an orange, what responses might be evoked? There is no way for an observer to predict with certainty how such a child would respond, though it is known that the greater the hunger of the child, the more likely is he to respond by eating the orange. The consummatory pattern of eating is said to be sensitized by the need drive of hunger. Similar sensitizing of appropriate responses occurs under other drives.

The above brief and simplified discussion of selecting stresses the need drive arising from deficit of foods. Other demonstrations have shown that changes in the internal environment are frequently followed by differential sensitization of the organism. Emphasis in the following discussion of selecting will continue to be upon those motivational determinants which owe their origin to variations in the internal environment.

Being sensitized for a particular external stimulus does not mean that the organism will inevitably change his responses. An organism may shift in his focusing upon various objects in the external world, but his response patterns may not markedly shift. Usually, however, whatever produces a shift in the readiness of the organism for a particular stimulus input in contrast to another likewise affects the mechanisms concerned with the selective releasing of behaviors. This same point may be phrased as follows: when the figure of the perceptual field changes, so usually do the responses.

Changes in Sensitization to External Stimuli

Instincts are released into behavior under the influence of sign stimuli (see p. 57ff.), but unless the organism is *ready* to be affected by these stimulating events, their mere presence in the external world is not inevitably followed by any instinctive behavior. In other words, the instinct is more likely to be released if the organism *is* primed by internal conditions to relevant sign stimuli. Even incomplete sign stimuli will release an instinctive pattern, as mating, when the animal is internally ready for the release: "Males in sexual condition become more and more ready to mate with suboptimal substitutes of females when they are not allowed to mate with an optimal female of their own species" [80, p. 119]. Hoarding, often classified as an instinct, is affected by the immediate need drives. The hungry rat, for example, does not hoard nesting materials but will chiefly hoard food pellets; and rats which are thirsty will store cotton-wool balls from which they can later suck water.

Self-selection among Foods. A well-developed series of studies concerned with the self-selections among a variety of food elements—protein, fat, vitamins, etc.—demonstrates that specific nutritional needs will differentially affect the readiness of the organism to respond to the various foods [98]. Studies with chickens, rats, pigs, and children report correlations between specific need drives and selected food elements. In general, the cafeteria feeding experiments indicate that animals are more ready to select foods which reduce their specific needs than those which do not, though some failures to select in line with needs are reported. The investigations of Richter indicate that this readiness of animals for certain external stimuli also varies when the endocrine balance is disturbed. An example is the well-known increased readiness to select salt after the disturbance created by adrenalectomy [69]. The animals after the operation change remarkably in their responsiveness to this substance. When placed in a choice situation between two drinking bottles, one with plain water, the other with a salt solution, the animals greatly needing salt ingest more of the sodium chloride solution than of the plain water. These animals appear to have a greater preference than normal animals for even a slight trace of the substance in the solution. As seen in the first two studies of Table 5-1 the *preference threshold as determined by choice responses* is lower for the animals greatly needing salt than is the threshold for normal animals.

What are the mechanisms permitting varying selections of different external stimulating agents? A more specific question: how do the body needs affect the selections among food substances? Richter [69] suggested that the variations in responsiveness to foods as needs change could be traced to lower thresholds of taste *receptors*. This interpretation of the selections of needed substances is, however, challenged by studies using another method of detecting thresholds. As described in Chapter 4, threshold differences may be also detected by the electrophysiological technique. Essentially this method permits in the case of taste receptors the recording of the afferent nerve discharge following stimulation of the tongue by different solutions. As seen in Table 5-1, Pfaffman and Bare [62] using this method found no difference in thresholds for sodium chloride between the normal subjects and those greatly needing the substance. The normal animals sense even a slight trace of salt in a water bottle; however, they do not drink more frequently from this solution. On the other hand, the operated animals, though needing the salt, do not detect the substance in any superior fashion. Note, however, that they select it more frequently. Their greater responsiveness to the sodium chloride substance is therefore not the sole result of a greater excitability of the taste receptors. This finding is, of course, in contradiction to Richter's hypothesis. Whatever are the selecting mechanisms permitting varying responsiveness to different stimulating sources in the external field, they are apparently centrally located. Possibly specific need-drive components affect directly the selecting mechanisms.

In addition to specific need drives, at least two other variables influence food preferences: (*a*) learning and (*b*) the characteristics of the selected objects. As seen in the last two studies in Table 5-1, reward and punishment permit a finer discrimination than previously attained between plain water in a drinking bottle and a solution with a slight trace of salt. In another line of experimentation, Young [98, 99] has shown that the characteristics of the selected food objects—their texture, color, flavor, and others—are significant in the choices of organisms. In fact, Young has suggested that likes and dislikes are influential even in selections by subhuman animals. Many organisms have strong and fairly stable preferences among foods. For example, the readiness to accept pure sucrose is found among such diverse animals as the horse, dog, rat, bear, skunk, racoon, spider, snail, slug, and many species of insects [95]. This liking for sucrose can be demonstrated whether the subject has or has not a specific body need for the substance. The established preference for

Table 5-1

Sodium Chloride Thresholds, Determined by Different Techniques, for Adrenalectomized Rats Greatly Needing Salt and for Normal Animals

Investigation	Normal animals	Adrenalectomized animals	Techniques
Richter [69]	0.055	Threshold lowered	Preference threshold determined by choice responses
Bare [7]	0.06	Threshold lowered	Preference threshold determined by choice responses
Pfaffman and Bare [62]	0.008	Threshold unchanged	Electrophysiological technique *
Carr [14]	0.009	Threshold unchanged	Preference threshold determined by choice responses, with shock as punishment
Harriman and MacLeod [36]	0.002–0.000025	Threshold unchanged	Preference threshold determined by choice responses, with reward and punishment

* Pfaffman points out that in recording nerve discharge from the chorda tympani nerve "we are sampling only a portion of the total sensory field, namely that arising from the anterior tongue surface" [63, p. 20].

saccharin, a non-nourishing material, also illustrates selections which are not dependent on specific need drives.

Both stable preferences and the changing qualitative needs for food elements are interacting variables affecting the choices. Young [99], who has been particularly concerned with factors involved in stable preferences of foods, maintained rats on an "adequate prepared diet." At the age of 101 days, the animals were given individual tests of preferences between all pairs of the following foods:

Fresh milk standardized at 4 per cent butterfat (M)
Pure butterfat, free from salt, prepared for the experiment (B)
Cane sugar, granulated, extra fine (S)
White flour made from wheat (F)
Whole-wheat flour, from selected wheat, ground for the experiment (W)
Dehydrated milk, a commercial powder (known as Klim, which is milk spelled backwards) (D)

Table 5-2

Rat number	Preferential sequence					
40	S	M	W	D	B	F
41	M	S	W	D	B	F
42	M	S	D	W	F	B
43	M	S	D	W	F	B
44	M	S	W	D	B	F
45	M	S	W	D	F	
46	M	S	W	D	F	B
47	M	S	W	D	B	F
48	M	S	W	D	F	B
49	M	S	W	D	F	B

SOURCE: Reprinted by permission from Paul Thomas Young, Motivation of animal behavior. In Calvin P. Stone (ed.), *Comparative psychology* (3rd ed.). Englewood Cliffs, N.J.: Prentice-Hall, copyright, 1934, 1942, 1951.

As a result of the paired comparison tests, the foods could be arranged into a "transitive series from the most to the least acceptable." As seen in Table 5-2, this group of ten rats prefers milk to sugar, with both of these being more acceptable than whole wheat, etc. In repeated experiments, the arrangement of most acceptable to less preferred is "relatively stable for a given set of experimental conditions but *it can be changed by changing the diet*" (italics added) [99, p. 75]. Preferences for specific foods are not entirely independent of tissue needs.

Concluding, it can be said that the responsiveness of organisms to the stimulating agents of the external world is influenced by drive components. The limited evidence briefly reviewed above for this conclusion shows (*a*) there are changes in responsiveness to sign stimuli as the internal environmental conditions are varied, and (*b*) there are reported correlations between specific need drives for food elements and selections among such substances.

The discrimination of various aspects in the external world determine what *can* be selected. It is necessary to discriminate differences before there can be selective responsiveness. Discrimination, however, does not force a choice. As Pfaffman and Bare [62] demonstrated, the normal animals had their receptors aroused by the mere trace of salt in their drinking water, but not being in any great need for the substance, they did not respond to this salt substance in any greater degree than to plain water. We next briefly consider selecting among potential responses.

Changes in Sensitization in Respect to Potential Responses

Organisms have potentially many different responses. They may be described in general terms, as *approach* or as *withdrawal*. They may be quite specific unlearned responses, as *tropisms, reflexes, instincts,* or such specific *learned responses* as "running down an alley" or "pushing a lever." Many variables are involved in what is the actual performance in a particular situation. In the few illustrations presented below, attention is given to some of the correlations between body chemistry and observed behaviors.

Dominance and submission represent identifiable response systems observed in such organisms as chickens, dogs, monkeys, chimpanzees, and men. The behavior patterns identifying a dominance-submissive hierarchy are specific for the species observed; in general, dominance represents some kind of social control over others. Figure 5-13 illustrates a dominance hierarchy in a small group of preadolescent male rhesus monkeys. Among the many determinants influencing whether an organism will be dominant or submissive are (*a*) the degree of hunger and (*b*) the sex hormonal level. The dominance-submissive relationship in pairs of chimpanzees shifts according to the degree of food deprivation. In a study of the effect of a semistarvation diet on adult human males, it was observed that they also were more easily irritated as their hunger increased. Since the subjects in this study were volunteers, there was, however, no extreme aggression against the experimenters who were withholding the food [45].

Aggressive behavior is likely to appear as the amount of male hormone is increased in an organismic system. Fighting is increased in fishes, reptiles, and birds by androgen administration. Castrated male rats show increased signs of aggression under administration of large doses of male hormone. Though there is a positive correlation between the degree of aggression and the level of male hormones in primates, it is not as consistent a relationship as in the infraprimates [55]. Of course, men and probably chimpanzees are capable of indirect and subtle learned methods of responding aggressively.

Beach [8] reports studies with females of lizards, rats, and chickens when a change from the female to the male mating response pattern occurred following injection of the male hormone. Note that the external stimulating field remained unchanged, at least objectively. The shift in the response pattern apparently resulted from a change in the internal environment and a consequent effect on the drives of the organism.

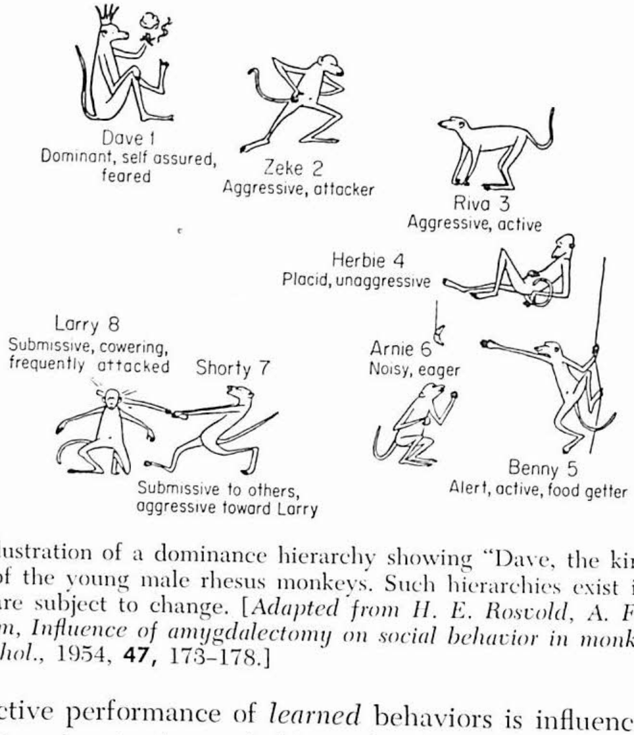
Dave 1
Dominant, self assured, feared
Zeke 2
Aggressive, attacker
Riva 3
Aggressive, active
Herbie 4
Placid, unaggressive
Larry 8
Submissive, cowering, frequently attacked
Shorty 7
Arnie 6
Noisy, eager
Benny 5
Alert, active, food getter
Submissive to others, aggressive toward Larry

FIG. 5-13. Illustration of a dominance hierarchy showing "Dave, the king" to "Larry, the lowest" of the young male rhesus monkeys. Such hierarchies exist in other social groups and are subject to change. [*Adapted from H. E. Rosvold, A. F. Mirsky, and K. H. Pribram, Influence of amygdalectomy on social behavior in monkeys. J. Comp. Physiol. Psychol.*, 1954, **47**, 173–178.]

The selective performance of *learned* behaviors is influenced by motivational determinants. As need drives change, so does the learned performance, i.e., other things being equal. In two studies [50, 66] the strength of a habit is controlled in order to test for the influence of need drives in the selective evocation of the learned response systems. The specific problem is as follows: when rats are well trained "to run one path to food when hungry" and "to run the alternate path to water when thirsty," what will be the effect on performance of combined hunger and thirst? Various combinations of deprivations are tested, such as 30-hour hunger with 12-hour thirst. The general answer to the question is that the stronger need drive in the combination sensitizes the habit associated with its reduction. In the case above, the animals would run down the path to food under the 30-hour hunger.

Motivational determinants are constantly influencing stimulus and response selecting. In the few illustrations cited above, attempting to test for their influence, the complexity of the factors involved becomes apparent. It can at least be concluded that as the drives shift in strength so do the selections of the organism.

The discussion of the final facet of motivation to be considered in this chapter—direction—cannot be divorced from the problems involved in understanding variations of activity-level nor in selecting. Two additional questions are, however, considered in the next section: what permits the organism to move toward *ends*, and, after learning, toward *anticipated goals*?

DIRECTION

The first problem of direction concerns the mechanisms by which naïve organisms continue to be oriented over several choice points and often, in spite of variability, attain *ends*. For example, a simple organism, as a spider, starts a series of responses which continues with some variability but ends with a completed web. And birds build nests which differ according to the particular species to which they belong. In the construction of the nest there is variability. No nest is built in exactly the same order of responses, but finally the species-related object is attained. The object constructed is not essentially different from nests built by others of the same species.

What is called the *end* to a series of responses may be described as an object, a place of a certain character, a consummatory response, or perhaps as relief, provided that there is a need drive to be relieved. However described, the significant point is that simple animals, even in their first construction, seem to be directed toward ends which when attained mark the completion of an act. Another illustration, in Chapter 3, is the behavior of a wasp storing in a burrow a caterpillar, future food for future wasps. Before the wasp's eggs are deposited upon the caterpillar, all responses of the insect seem directed to this end. The insect proceeds through a fairly complicated series of responses, varying according to the external field in which she is working; finally the eggs are deposited, and the burrow closed in such a fashion that it is concealed. Then the insect flies away. Though various interpretations have been advanced for similar acts, it is generally granted that their completion can be identified in the continuous activity streams of animal forms. On the basis of such observations, it is said that organisms exhibit directionality.

Directions without Learned Goals

Sensory Deficit. What are the mechanisms permitting directional control in simple, and even in completely naïve animals? One suggestion (attributed to Lashley) is that a simple organism (or also higher animal forms) may respond to the absence of stimulation. What is lacking may be necessary for the survival of the animal or of the species. In any case, the organism is assumed to suffer from a sensory deficit, as a spider might be disturbed by the absence of the stimulating pattern from a web. Under the influence of the sensory deficit, the insect would start weaving and presumably continue until a complete and appropriate web appeared. Thus the stimulation therefrom would remove the sensory deficit. Or a bird would start to build a nest under a sensory deficit. Let us assume that the bird places the sticks and straws in such a manner that the appropriate nest for his species is *not* emerging. Presumably at this point, or perhaps later, the bird would change the construction until finally the species-related nest appeared. The stimulation therefrom would then remove the sensory deficit which originally initiated the nest-building activity.

James [43] uses the concept of *sensory deficit* in interpreting direction when no construction is involved. James is interested in the orientations of newborn (still blind) dog puppies. One pup is removed from the litter and placed at a standard distance from the group, with the head of the isolated pup facing away from the group. The isolated pup moves, often away from the group, and continues to move for as long as 5 minutes, unless the "mother" or a member of the litter is tactilely contacted. This sensory contact removes a tactile and probably a temperature deficit which is considered the basis for the previous restless motion. A significant point is that if the isolated pup is touched on any part of his body, he orients toward the source of stimulation. Even if touched on the rear end, the isolated pup tends to rotate 180 degrees and then pull toward the spatial locus of the directing stimulus. Though a rolled paper or towel can be used to direct the blind animal spatially, the most satisfactory stimulus is another member of the litter. These three illustrations with spider, bird, and dog indicate that a control over variability *may* be traced to the absence of some necessary stimulating pattern.

Directional Cues from Sign Stimuli. Variability so that ends are attained may be controlled by sign stimuli present in the external field. Tinbergen [79] reports how the swimming of a simple animal (*Daphnia*) is directed by means of an external stimulation. These organisms (minute freshwater crustaceans) respond positively to light and generally move upward to the surface when the water is polluted. The surface of the water, being in contact with air, is relatively rich in oxygen. The excess carbon dioxide in the polluted water is said to release the movements; the light directs the animals. In order to illustrate directional control so that a nonadaptive end is attained, the experimenter may place the light at the bottom of a glass tank. At the same time he introduces excess carbon dioxide. The organism is released into action by the polluted water and is directed by the light. He swims downward and, in this artificial situation, is directed against his own survival. An end is attained, but in this case it is nonadaptive.

The distinction between releasing and directing stimuli is also made in the reports on the orientations of young birds (nestling thrushes). When still blind, the young birds release the well-known open-mouth response when stimulated by a movement of the nest. When the parent birds return with a worm (it is hoped) or some food object and jar the nest, this stimulation releases the open-mouth response by the nestlings. The *direction* of the movement is not, however, toward the parent bird. It is straight upward and said to be an orientation to gravity [79].

The two suggestions outlined above in regard to possible ways by which naïve organisms are directed toward ends never before attained by them are not independent of each other. In fact, it might be possible to say that the first (reaction to sensory deficit) is a special case of the second (control by sign stimuli). The third, now to be presented, is a general answer in regard to direction, and it could encompass the first two suggestions.

Direction Controlled by Sensory Feedback. No attempt will be made herein to evaluate the usefulness of the analogies drawn by the cyberneticists between the activity of machines and of organisms. However, it is generally granted that direction in a series of responses may be related to the feedback (aftereffect) following each response. A simple illustration is the behavior of a hunting animal on the trail of another creature. As long as the animal is on the trail the sensory feedback is unchanged, but if he loses the scent, then the sensory aftereffect is changed. He then starts exploring *as if* he were disturbed by the shift in the feedback after each response. His direction, however, appears to remain unchanged; at least, a renewed contact with the trail immediately arouses the continuation of the hunting behavior pattern.

Visual tracking is frequent in man's activity stream. Mechanical control systems may be substituted for the trial-and-error attempts which a man makes in following a moving target. Any such control system has what the hunting animal or the tracking man must also possess: some mechanism permitting a comparison of the feedback following his responses to the position of the target. When the comparison indicates that there is a divergence between his position and the target, then there is an error.

There are, however, two aspects to the tracking task: the first, described above, is the *comparison*. Next, *if* there is an error, there must be an *attempted correction*. When corrections are not attempted, then the organism is no longer directed. In any directed series of responses there must be some kind of error-identifying and error-reducing mechanisms.

When an organism is dominated by a need drive, as pain, errors may be identified whenever the aftereffect from the responses is an increase in the need drive or, at least, no relief from it. For example, assume an organism is placed under continuous injurious stimulation. If the aftereffect following the first responses is not a diminution of the injurious stimulation (and of the pain), the response is an error. Then organisms act more variably until a response is finally followed by relief. Learning may also take place during such a regulatory act. Direction in the stream of activity is not, however, solely dependent upon learning.

Possible directional mechanisms which permit a control in a series of responses of simple or complex organisms so that finally an end is attained were briefly reviewed above. There was no assumption in these descriptions that the organism anticipated the end toward which it moved. In fact, it might be entirely naïve in regard to where it was moving. It might under some circumstances attain a nonadaptive end. In the illustration above, *Daphnia* were directed to a nonadaptive end. They were moved in an artificial environment, created by placing the light under the water tank, to their own destruction. Being oriented by the light, an "error" to them was a response which did not lead to the light.

Direction Influenced by Anticipated Learned Goals

In a previous discussion of activation, it was pointed out that organisms are incited by goals, i.e., they are energized by anticipated acceptable effects. In addition to the energizing, goals also have other functions. For example, orientation by a symbolized goal may influence through a series of choice points the organism's direction toward the reattainment of the actual goal. A few observations support this hypothesis that both infrahuman organisms and men may be directed by symbolized goals. (*a*) A hungry rat, having run to a reward box several times, may escape from the confining maze walls and go directly toward the goal place where he again obtains food. (*b*) An animal may vary his paths in an open-alley maze, though he avoids moving from the entrance to the exit by long routes. In other words, he seems to be oriented by a learned goal rather than running off a learned habit. He may take various routes from the entrance of the maze to the exit (see Fig. 5-14). (*c*) Observations of detour behavior around a barrier show how organisms can turn away from stimulation of the goal object (as food) and yet continue to be under its influence. They behave *as if* the goal were present in their immediate field. In their detouring, they have not forgotten the goal. Some representation continues to steer them. (*d*) Another observation supporting goal orientation as a directional influence is any consistent selection of the shortest available path to a rewarding effect, "practically regardless of previous practice" [41, p. 304]. When an animal selects a path to a goal which is not necessarily the route with the greatest practice, his behavior suggests that he is under the influence of goal orientation and not merely acting on a motor habit.

Place learning, described in Chapter 7, supports goal orientation. When an animal has learned various places in an external field, he is capable of moving away from or toward such locations. If his movements are related to previous acceptable effects at some particular location, then he appears to be goal oriented. This conclusion seems more pertinent if there is no opportunity for him to be stimulated by the reward, that is, if he cannot smell nor hear nor see it.

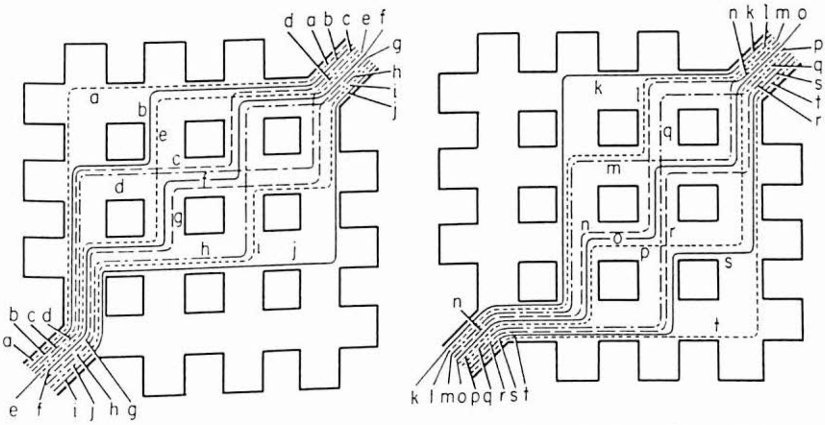

FIG. 5-14. Dashiell's open-alley maze for studying goal orientation. All possible errorless runs (twenty in number) are indicated from entrance into the maze to the exit and goal box. [*From J. F. Dashiell, Direction orientation in maze running by the white rat. Comp. Psychol. Monogr.*, 1930, **7**, *no.* 32.]

Summary. To be directed toward ends is characteristic of organisms, but the mechanisms which make this possible are not clearly understood. Certain possibilities are suggested. When an organism, simple or complex, moves toward an end never before attained by him, he is possibly directed by (*a*) attempts to remove a sensory deficit, (*b*) responses aroused by sign stimuli, (*c*) corrections of error after feedback from the responses. Learning may occur in any directed act and presents its own particular problems.

Organisms capable of learning may symbolize acceptable effects previously received after certain responses and/or after certain stimulations. These learned anticipations permit goal orientations. Some limited evidence was reviewed that such inferred central events may influence the choices of organisms through a series of selections so that a former goal is reattained.

A CONCLUDING STATEMENT

In conclusion, the motivation of organisms may be viewed in many different ways. In the biological approach to motivation within this chapter—a view which perhaps would be better described as a neobiological view—it is assumed that all organisms are continuously active. They, of course, vary over time in the degree of their activity. Some of the drives responsible for the rises and falls in activation-level were first reviewed.

Motivation is not simply the energetics of organisms. Attention was given to motivational determinants as influential in the selections of organisms. Finally there were considered the possible mechanisms permitting control over a series of choice points so that ends and learned goals are reached. This is perhaps the most difficult of the three general problems considered here.

The neobiological view of motivation can be compared to an older approach to motivation which has influenced psychology for some time. In the older biological view, tissue inadequacies (or their learned surrogates), were called the mainsprings to activity. In the neobiological view there is a recognition of the significance of variations in the internal environment, but it is not assumed that all excitability, all drive tension, has as its basic source the tissue disturbances.

Another important modification of the need-based approach to motivation is the denial that the "regulatory act" is the prototype of all motivated behavior. Descriptions of the "regulatory act" are frequent. Its stages are familiar to psychologists: first, the initiation of the act under some kind of maladjustment, then random trial and error, and finally, alteration of the external environment (or of the organism) so that relief from the maladjustment is obtained. Then the organism is said to be adapted (adjusted); the "regulatory act" is completed. There is no doubt of the reality of such acts. Dashiell [18] described the stages of regulatory behavior of diverse animal forms: the amoeba, paramecium, stentor, turtle, earthworm, rat, and man. However, such description is often too gross for much understanding. It is like trying to untangle the determinants of the movements of atoms by merely watching an explosion. It is essential to isolate the different functions of motivational determinants in all behaviors. Therefore, the role that need drives and other drive components play in the activation of organisms were considered *independent* of their other functions. Then their roles in selection and direction were briefly outlined. By this method, it is hoped that the complexity of events which is subsumed under that vague phrase, *motivational changes*, may be illuminated.

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CHAPTER 6

Acquired Drives and the Curiosity-investigative Motives

Most studies on animal motivation have been confined to the biological or homeostatic drives that were discussed in the previous chapter. This emphasis on drives such as hunger and thirst has been a source of criticism leveled at animal psychologists by those interested in human motivation. The argument is that most human behavior does not seem to be directed toward the satisfaction of basic biological needs. In our culture, severe hunger or thirst, for example, is an atypical condition. Society is organized to provide for the fundamental necessities of life.

Rather than basing a theory of human motivation on the drives investigated in the animal laboratory, some psychologists have proposed a different level of conceptualization. Many motivational theorists, for instance, maintain that the need for self-actualization, the need to know and understand, the need for belongingness and love are vastly more important in modern society than are the biological needs. At first glance it may appear that animal research can make little or no contribution to a comprehensive theory of motivation, since, according to these theoreticians,.the motives of man are entirely different from those of lower animals. It should be made perfectly clear, however, that animal behavior is not based exclusively on the so-called "primary biological drives." These particular drives are most frequently utilized in the laboratory because they can be controlled while the investigator focuses his attention on some other phenomenon, and for decades it usually has been the phenomenon of learning. Indeed, nearly every important problem in learning can be studied by observing how a hungry rat, cat, or monkey obtains food under different experimental conditions. It is almost as if the motivation of animals has been exploited rather than investigated. But recently some animal psychologists have become interested in motivation as an area of investigation in its own right, and their research shows decidedly that motivational mechanisms other than the primary biological drives are important determinants of behavior. Others, while working on the problem of motivation, are essentially extending the previous research on learning. This chapter will describe some experiments resulting from these two different approaches.

In the following sections the operation of a drive or motive is inferred when new responses are learned and persist for reasonably prolonged periods of time without recourse to primary reinforcement such as food or water. These criteria for postulating the presence of a motivational state are not precise. Nevertheless, they are explicit in the writings of many researchers in this area and are also fundamental to the design of the various experiments. The distinction between drive and motive is, of course, arbitrary. The term "drive" will be used here when the behavior under investigation is conditioned upon one of the primary biological drives. The term "motive," on the other hand, will be employed when there is no relation between the observed behavior and the operation of known biological drives.

The reader may be familiar with the position which contends that there is no necessity for postulating drive or motive in order to predict behavior. In other words, knowledge of the past history of the organism and control over the existing stimulus events are sufficient to account for the observed behavior. It is the belief of the writer, however, that the concepts of drive and motive led to the formulation of many of the studies reported below, which otherwise might not have been carried out. At the very least, many of these experiments represent a refreshing change from the type of research that has been conducted on animal motivation in the past. Once the experimental data exist, there is no real objection to discarding drive or motive as an explanatory concept for these data. In fact, this approach may be preferable, since many entanglements involving the nature of drives and their interactions can be eliminated. Notwithstanding the advantages of a purely descriptive system for handling the experimental data, the procedure adopted in this chapter is one of organizing the data within a framework of the different postulated motivational mechanisms—a procedure customarily followed by other researchers who address themselves primarily to the problem of motivation.

ACQUIRED DRIVES

A persistent problem in the field of motivation has been that of accounting for the vast complexities of behavior in a parsimonious manner. Early psychologists attempted to explain behavior in terms of various instincts. At first, only a few instincts were proposed, but in time the number increased beyond all reasonable bounds and the doctrine of instincts lost whatever explanatory power it had earlier possessed. Most psychologists today would deny that it had ever possessed any explanatory power at all. Actually, the current treatment of human motivation is not very far removed from this earlier approach. Segments of behavior are labeled, and the labels are then accepted as if they were real phenomena based on sound experimental data whereas, in fact, they usually are not amenable to experimental verification.

One prominent notion held by many motivational theorists, that *is* directly testable in the laboratory, is the belief that drives can be acquired or learned. By incorporating the concept of acquired drives into motivational theory, the psychologist can accept the thesis that there is a limited number of primary biological drives underlying behavior. At the same time, he can account for the complex behavior which, without knowledge of the organism's past history, appears to be independent of the biological drives. From this frame of reference, drives for money, prestige, power, love, and countless other proposed drives which seem important for motivating man fall within the province of learning. And, at least on the surface, the phenomenon of learning appears to be a reasonable way of interpreting these forms of behavior. After all, we know fairly well the conditions necessary for establishing learning, but we are quite ignorant of the mechanisms behind the aspirations for power, social acceptance, or knowledge.

Acquired Avoidance Drives

The classic experiment demonstrating the existence of acquired drives was conducted by Miller [41], who chose fear as an area for study. The literature on abnormal psychology is replete with the notion that fear, or anxiety, is a compelling motivational agent underlying the avoidance of anxiety-producing situations. Miller hypothesized that if fear had drive properties, then animals should learn responses that would lead to the reduction of fear. His approach to the problem was simple and direct. Rats were placed in a box consisting of two compartments. One compartment was painted white and the other black. After it was ascertained that the animals had no preference for either compartment, they were placed in the white compartment and subjected to a series of electric shocks. Escape from shock was possible by running into the black compartment. A barrier was then inserted between the two compartments, thus preventing escape. A wheel, however, was located adjacent to the barrier, and by rotating the wheel through a small arc the subjects were able to cause the barrier to drop. The important finding in this study was that rats learned to turn the wheel and enter the black compartment even though no additional electric shocks were administered.

Miller next sought to find out whether responses to the wheel could be extinguished and a different response learned. A bar was placed near the wheel, and by pressing the bar instead of turning the wheel the barrier was made to drop. The rats, still receiving no more shocks, soon learned to respond only to the bar. Presumably, the animals learned to fear the white compartment because of its previous association with pain. That this acquired fear had drive properties was demonstrated by the fact that rats learned responses which, according to Miller, led to the reduction of fear, i.e., they learned to attain a sanctuary in the black compartment. The learned responses under these test conditions are relatively persistent, since several hundred trials without the primary reinforcement of electric shock are sometimes required in order to extinguish them [42].

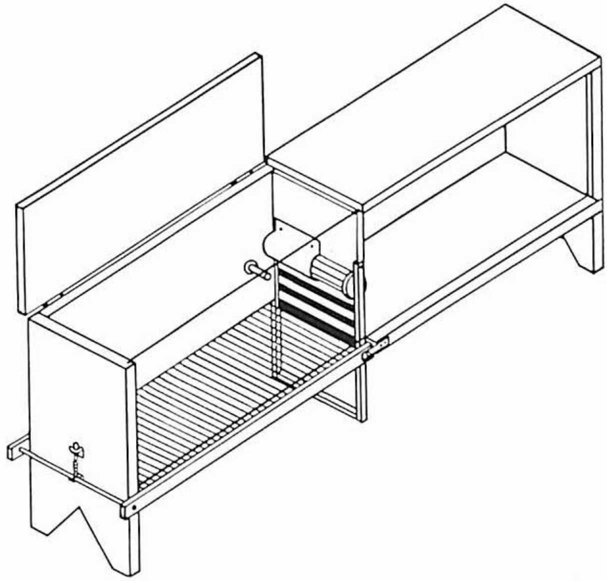

FIG. 6-1. Apparatus used to establish a learned fear drive. The learned responses consist of turning the wheel and later pressing the bar to attain entrance into the adjacent (safe) compartment. [*From N. E. Miller, Studies of fear as an acquirable drive. I. Fear as motivation and fear-reduction as reinforcement in the learning of new responses. J. Exp. Psychol.*, 1948, **38,** 89–101.]

Brown and his associates [10] have demonstrated another behavioral consequence of acquired fear. Using rats, they first carried out the steps necessary for the acquisition of fear. A previously neutral stimulus (a combination of buzzer and light) was presented for 5 seconds. Near the end of this interval the animals were given an electric shock. To establish fear in the rats for the buzzer-light stimulus, the animals were subjected to this sequence of events several times. When a loud sound was later substituted for the electric shock, the subjects exhibited a startle response to the sound which was much more vigorous than that normally observed. The experimenters believed that the buzzer-light stimulus produced fear which, in turn, served to augment the size of the startle response. Or, in other words, the increased magnitude of the startle response was attributed to the energizing or drive properties of acquired fear.

The results of other studies have also supported the thesis that acquired fear can act as a drive [9, 25]. Furthermore, it looks as if the learning of fear were influenced by the same factors that govern the learning of other responses. Generally speaking, the strength of a learned response is directly proportional to the number of reinforced trials and inversely proportional to the number of nonreinforced trials.

Kalish [35], with an excellently designed experiment, was able to demonstrate these functional relations for acquired fear. He conditioned rats, housed in a small compartment, to fear a combination buzzer-light stimulus by pairing it with electric shock. Some animals received twenty-seven paired presentations, whereas others received nine, three, or one pairing of buzzer-light and shock. Following the acquisition trials, he gave the animals varying amounts of extinction trials by presenting the buzzer-light stimulus alone.

To measure the drive strength of fear, the animals were tested in another apparatus which consisted of two compartments separated by a low hurdle. One of the compartments was identical with that employed in the acquisition-extinction training; the other was not. The rats were placed in the identical compartment, and the time taken to jump to the other compartment after presentation of the buzzer-light stimulus was used as the index of the strength of fear. The underlying assumption was that the rapidity with which the rats crossed to the opposite chamber was directly related to the strength of the fear drive. Figure 6-2 shows the influence of the number of acquisition and extinction trials on acquired fear. The data in this figure are arranged to show the effects of acquisition training and those of extinction training separately. And it is seen that the strength of fear depends upon the number of electric shocks received as well as upon the number of times the electric shock is withheld. The results obtained on the second test day show similar trends, but differences between conditions are not as marked. In summary, Kalish's findings rather convincingly place the fear drive directly in the field of learning.

The conditions under which fear or anxiety can be learned have been made explicit through animal studies and provide a way for interpreting the more complex behavior of man. Brown [8] has offered a suggestion on the manner by which the acquired fear drive might be the basis of the so-called "drive for money." Actually, he could have taken any of the proposed acquired drives that indicate the functioning of an anxiety component. He, however, settled on the money-making drive, and his argument is as follows:

Occasionally, a child experiences physical pain either through illness or some type of accident. At these times, by facial expression or tone of voice, the parents express anxiety. Subsequently, the problem of money may arise, and the parents again may show similar anxiety reactions. For example, they may remark fretfully on the lack of money or that a certain object costs too much. The child experiences the anxious behavior of the parents, previously associated with his own physical discomfort, in situations where now the shortage of money is concerned. Through higher-

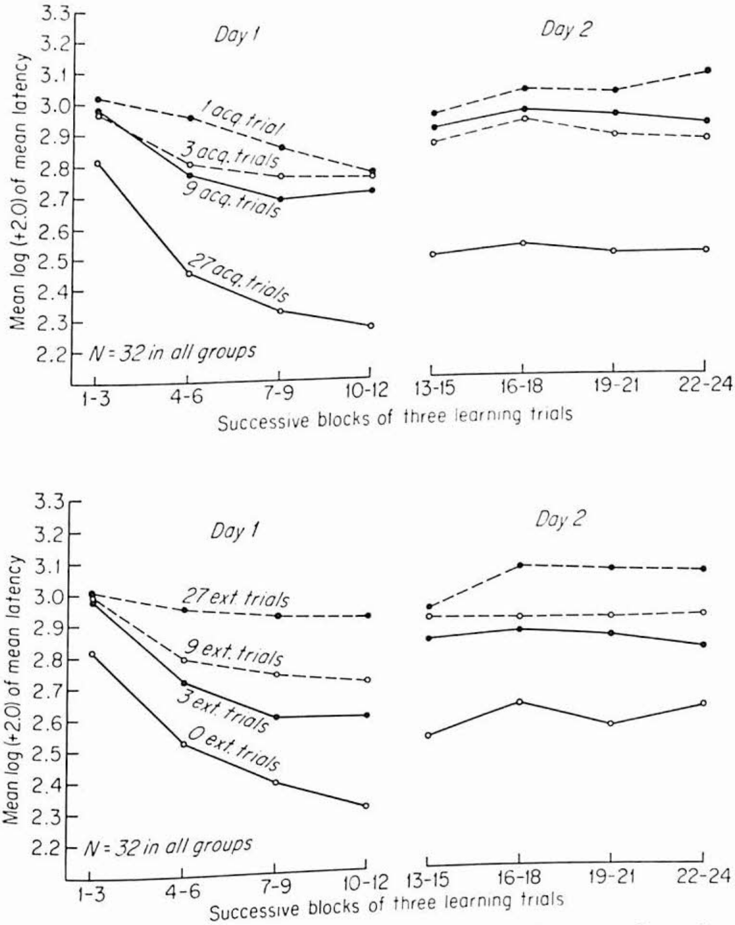

FIG. 6-2. The influence of number of acquisition trials and the number of extinction trials on the learned fear response is illustrated in the upper and lower graphs, respectively. Response latencies serve as the index of the strength of fear. [*From H. I. Kalish, Strength of fear as a function of the number of acquisition and extinction trials. J. Exp. Psychol.*, 1954, **47**, 1–9.]

order conditioning, the child's anxiety becomes elicited when there are not sufficient funds to buy some desired item. By extension of this line of reasoning, actual receipt of money would serve to reduce anxiety. Behavior suggestive of an acquired drive for money may essentially be a means for reducing fear or anxiety arising from the lack of it.

Brown's attempt to explain the motivational basis of money-making behavior is, of course, highly speculative. This type of analysis, however, makes a certain amount of sense, and it has the added virtue of being related to the findings of well-controlled laboratory experiments.

Acquired Approach Drives

The notion of acquired fear has commanded the interest and respect of many psychologists because of the support it received from animal studies and the relevance of acquired fear to the understanding of man's behavior. When placed in its proper perspective, however, acquired fear probably can account for only a fraction of the total activities of man and lower animals and perhaps a small fraction at that. Everyday observations clearly indicate that a great deal of behavior in lower animals and man is of the outgoing, positive type. Much of the time, organisms tend to seek rather than to avoid situations. Are there then acquired approach drives? This question is of sufficient importance to warrant some time tracing its modern history.

Long before the laboratory work on acquired fear, Woodworth, in his well-known book, *Dynamic Psychology* [60], sought to explain why people participate fully and regularly in activities that no longer serve to satisfy the basic biological needs. This seems to be the usual way in which man behaves and, if the primary biological drives cannot adequately account for the maintenance of behavior, what other motives may be operating and how do they come into existence? Woodworth's answer was that innumerable drives are responsible for approach behavior and that the drives are acquired. The way in which he dealt with drives makes any attempt to classify them meaningless. What was important was Woodworth's hypothesis about how drives are learned. His ideas on this subject were perhaps deceptively simple: Behavioral mechanisms ranging from purely mechanical skills to complex social skills are developed to cope with the many problems that confront us. Those mechanisms that can effectively handle a problem, but which are not executed automatically, possess a high interest value for the individual. There is a definite satisfaction experienced each time the mechanisms are used in connection with the particular problem. Those mechanisms become endowed with drive properties, i.e., they furnish their own force, so to speak, and can motivate behavior in situations other than those associated with the original problem.* An example frequently cited to illustrate Woodworth's notion of acquired drives is the case where a person enters business for economic gain so that he is able to survive. He continues, however, to work diligently long after he has accumulated enough money to live comfortably for life. There persists a lively and compelling interest in the many ramifications of the business after the original goal has been attained. Examples can be taken from all walks of life which illustrate man's active participation in events as an end in itself.

Allport's [2] principle of functional autonomy of motives, published several years after Woodworth's statement, is essentially another version of the idea that behavioral mechanisms may become drives. Here again, the problem attacked by Allport was the perennial one of why people act as they do. Allport believed that the motives of the adult can and do operate independently of the biological drives, although he conceded that there may be an historical connection between the adult's motives and those drives that govern infant behavior. With respect to acquisition of motives, Allport also suggested that behavioral mechanisms which effectively solve problems may acquire motivational properties.

Animal investigators have been actively engaged in collecting information on conditions responsible for approach behavior when that behavior is not immediately rewarded by the reduction of biological drives. There has been little or no disagreement on the question of the omnipotence of seemingly unrewarded approach behavior in both man and lower animals. Disagreement does exist, however, over the way in which this behavior can be best explained. Is it necessary to postulate the emergence of a new drive, or can approach behavior be explained in a more parsimonious manner?

Anderson [3] preferred to interpret his data in accordance with the acquired-drive theory. He ran hungry rats in a maze for food reward, then observed their performances in a different maze which contained no food in the goal box. His rats learned the second maze with little difficulty. In fact, after learning this one, some of the animals learned still another maze without food reward. Anderson proposed that in his experiment, the drive, originally based on hunger, became arousable by the external stimuli provided by the maze. He went on further to say that this externalization of drive is one kind of autonomous motive. A somewhat confusing aspect of Anderson's study was that experience in the maze for food reward was not a necessary prerequisite for learning the other mazes, since some rats were able to do so without this previous training.

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* In accordance with the distinction made between drive and motive at the beginning of this chapter, what Woodworth called a drive would be classified here as a motive.

By and large, most psychologists who work with animals have accepted a different explanation of approach behavior. They call upon the principle of secondary reinforcement to explain why animals perform when they are not immediately rewarded by food, water, or other biological necessities. Secondary reinforcement simply means that stimuli associated with a primary reward also acquire the properties of a reward, i.e., animals will work to receive these stimuli. Secondary reinforcing stimuli do not energize behavior; they merely reward behavior that is already in progress. According to this point of view, no new drive is postulated to explain approach behavior.

The experiments which support this position are quite straightforward and informative. Wolfe [59], working with chimpanzees, used a special vending machine which would dispense food each time a poker chip was inserted. The chimpanzees, with a little guidance from the experimenter, soon learned to work the machine themselves. Once they associated the poker chips with receipt of food, the subjects would work to get the chips. Their job was to pull in a weighted handle, whereupon they would sometimes receive a grape and sometimes receive a poker chip. The latter could be cashed in for grapes at the machine. The animals would quit working for the chips if food were not forthcoming. One of the more intriguing aspects of the experiment was that when the chimpanzees were forced to wait before exchanging the tokens for food, they would go along with this delay with less protest if they were permitted to keep the poker chips in their possession during the interlude.

Token-reward research with chimpanzees was carried further by Cowles [21], who demonstrated that the animals could learn several different types of problems for surrogate rewards alone. The incentive value of the tokens was, of course, dependent upon their exchangeability for food.

Saltzman [51] has shown that rats, too, will learn new responses for incentives having a secondary or derived reward value. He trained animals to run down a straight alley for food reward (Fig. 6-3*a*). Food was found only when a white goal box was present, although half of the time a black box was attached to the end of the alley. The white box should have acquired secondary reinforcement properties, since stimuli provided by it had been associated with the reduction of a primary biological drive, i.e., a hungry rat ate food. To see if new learning could occur on the basis of secondary reinforcing stimuli, the rats were next placed in a maze which contained no food (Fig. 6-3*b*). A white goal box was connected to one end of the maze, a black goal box to the other.

True to expectations, the rats learned to go to the white box. Sufficient controls were instituted to ensure that color preference or position of the box in the maze could not account for the obtained results.

In another study, again demonstrating learning to secondary incentives, rats were given food whenever a buzzer sounded. After 100 such combinations of food and sound, the subjects were placed in a box containing a lever. Each time the lever was depressed, a buzzer was heard but no food was received. The data clearly showed that rats learned to press the lever for sound reward [34].

A less striking but more thoroughly studied phenomenon is that already learned responses show greater resistance to extinction if a secondary reward remains in the test situation once the primary reward has been removed. To take one of the many examples of this type of experiment, food-deprived rats were trained to press a lever for food pellets. A click sounded concomitantly with depression of the lever. After the rats had learned the lever-pressing response, food reward was withdrawn but testing continued. Some of the animals still heard the click when they worked the lever, but for others the lever operated silently [11]. Apparently, the click served as a reinforcer, because those rats that continued to hear it after lever pressing was no longer rewarded by food responded more frequently than did the other subjects.

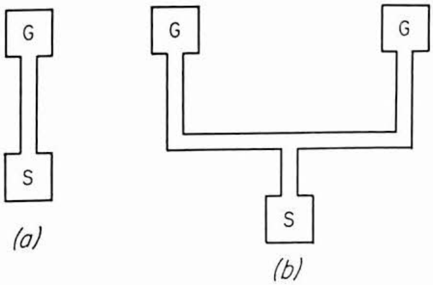

FIG. 6-3. 3*a* shows training apparatus; 3*b* shows testing apparatus. S and G represent the starting boxes and goal boxes, respectively. [*Adapted from I. J. Saltzman, Maze learning in the absence of primary reinforcement: a study of secondary reinforcement. J. Comp. Physiol. Psychol.*, 1949, **42,** 161–173.]

If secondary reinforcement can account for both the learning of new responses and the maintenance of already learned responses, the problem of the persistence of seemingly unrewarded approach behavior becomes one of searching for the secondary reinforcers that operate in the environment. Perhaps psychologists would go about this task more enthusiastically were it not for the fact that real doubts exist regarding the usefulness of the secondary reinforcement principle when applied to nonlaboratory situations. More specifically, approach behavior based on secondary reinforcement is extinguished unless primary reward is given at relatively frequent intervals. Outside the laboratory, and particularly with respect to human behavior, the receipt of primary reward appears largely to be incidental to the maintenance of ongoing behavior and the learning of new responses.

At the present time, the persistence of approach behavior cannot be adequately explained by the principle of secondary reinforcement, nor is there any convincing evidence to support the thesis that an approach drive operating independently of the so-called "primary biological drives" can be acquired. Possibly, what has been interpreted as indicative of an acquired approach drive in man may be a manifestation of other motivational mechanisms. Animal research relevant to the latter supposition will be discussed next.

THE CURIOSITY-INVESTIGATIVE MOTIVES

Until recently, the only drives that have been demonstrated in the animal laboratory have been the primary biological ones and acquired fear. Within this framework, we simply cannot give an adequate explanation for the almost insatiable curiosity of children or the strong and persistent exploratory behavior of animals. Consider, for example, the child's preoccupation with a new toy, a chimpanzee's or monkey's close examination of any novel item, a kitten's unflagging interest in small mobile objects, or a rat's continual investigation of an unfamiliar maze. To account for these forms of behavior in terms of hunger, thirst, sex, or temperature fluctuations is hardly satisfactory. In fact, it is most unlikely that these behaviors are even indirectly related to the so-called "primary drives." Nor is acquired fear of any great help as an explanatory concept, since these behaviors are directed toward rather than away from environmental stimuli. Something akin to curiosity appears to be operating. To postulate that curiosity-investigative motives are basic behavioral determinants, especially in higher animals, has a certain amount of face validity. As we ascend the phylogenetic scale, the biological drives play a lesser role in accounting for behavior, whereas exploration and manipulation appear to become progressively more important.

Research with Rodents

Maze Studies. Nissen's [50] research on the exploratory motive represents one of the first systematic studies in this area. To obtain an index of the strength of exploration, the Columbia obstruction box was used. This apparatus was frequently employed years ago for measuring the strength of various biological drives. The testing technique consisted of separating the experimental subjects (rats) from an appropriate incentive by an electrically charged grid (see Fig. 6-4). The number of times that the rats crossed the grid to obtain the incentive was taken as the measure of drive strength. By these means, the relative strengths of hunger, thirst, sex, and the maternal drive were recorded. Nissen was able to demonstrate the existence of an exploratory motive with this technique. A maze containing many alleys was substituted for the customary biological incentives, and the rats actually crossed the charged grill for the opportunity to explore the maze. All of the animals had had free access to food and water in their home cages, so any explanation in terms of hunger or thirst drives could not adequately account for the findings.

After Nissen's study, several years elapsed before exploratory behavior was directly investigated again. During this interlude, occasional references to the exploration motive were found in the literature but primarily in connection with the problem of latent learning. In these experiments, rats were run in a maze without any extrinsic reward. When food was later introduced into the goal box, animals that had had experience in the maze learned it more rapidly than did rats without prior experience. Exploration was postulated to explain the motivational basis for learning, but interest centered about the conditions underlying latent learning rather than those that elicit exploratory behavior.

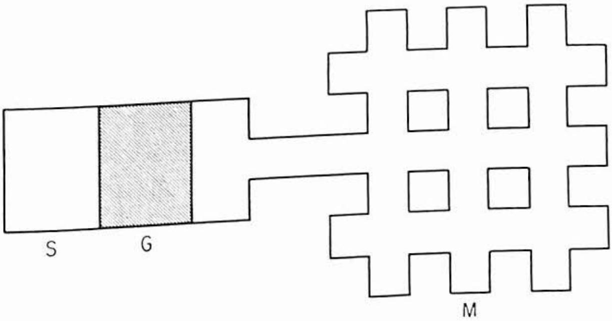

FIG. 6-4. Apparatus employed to study the incentive value of exploration. S represents starting box; G represents electrically charged grid; *M* depicts maze that serves as the incentive to explore. [*Based on H. W. Nissen, A study of exploratory behavior in the white rat by means of the obstruction method. J. Genet. Psychol.*, 1930, **37**, 361–367.]

The exploratory motive was again invoked to explain a frequently observed phenomenon in rat behavior called "spontaneous alternation." Rats that are run in a simple T maze possessing food reward in both arms of the maze tend to alternate choices between the two arms on successive trials. To explain this behavioral peculiarity, some investigators suggested that each response generated an inhibition to repeat the same response within a short time interval. Turning into the right arm of the maze, for example, would build up an inhibition for turning right, and the left turn would be favored on the next trial. Presuming that the rat did turn left on the second trial, the right turn would again be more probable for the subsequent trial.

Although it was proposed as early as 1925 that exploratory impulses might form the basis for alternate choices in a T maze [54], Montgomery [43] was first to investigate systematically the validity of the two explanations—inhibition generated by responses or exploration. Rats were run in a maze that was constructed in the form of a cross. Doors would be inserted just before the junction of the cross so that the maze could be partitioned into two T mazes with the same choice point but with different starting boxes. Each arm of this double T maze contained food pellets, an incentive absent in all subsequent studies to be discussed.

As diagrammed in Figure 6-5, alternating turns would lead the rats to the same place on each trial. Alternating places, on the other hand, would necessitate their making the same turns time and time again. The outcome of the experiment was that rats did alternate between places and not between turns. Montgomery interpreted these findings to signify that spontaneous alternation is nothing more than a special case of exploratory behavior. Rats, when tested in this type of maze, tend to explore that maze arm which was entered least recently.

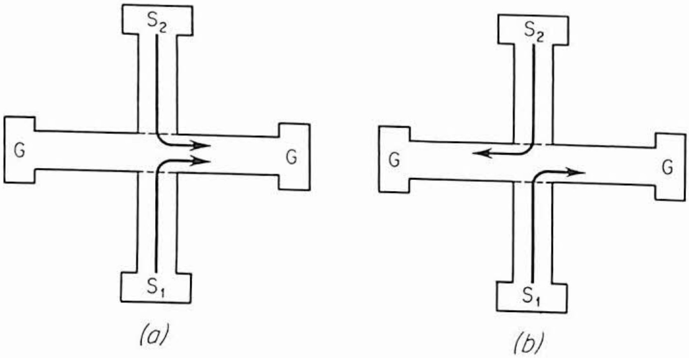

FIG. 6-5. 5*a* shows the consequences of alternating turns; 5*b* shows the consequences of alternating places. S_1 represents the starting box on odd-numbered trials. S_2 represents the starting box on even-numbered trials. *G* represents goal boxes, and the arrows show the hypothetical routes of the rat. [*Modified from K. C. Montgomery, A test of two explanations of spontaneous alternation. J. Comp. Physiol. Psychol.*, 1952, **45**, 287–293.]

Other investigators, while rejecting the inhibition explanation for spontaneous alternation, are nevertheless reluctant to accept any type of answer which rests upon an exploratory motive. Glanzer [24], for one, prefers to use the concept of "stimulus satiation" not only to account for spontaneous alternation but also for explaining exploratory behavior in general. What is meant by stimulus satiation can best be illustrated by considering a rat's alternate choice behavior in the T maze. When entering one of the maze arms, the animal is exposed to a particular stimulus configuration, and this exposure produces a satiation effect for those specific stimuli. Because of the satiation effect, the rat enters the other arm on the following trial. To provide for spontaneous alternation on successive trials, it is assumed that the stimulus satiation effect decreases as a function of time, and the animal will enter the maze arm associated with the least amount of satiation.

The difference between the exploration and stimulus-satiation explanations of spontaneous alteration may appear purely academic, since either can account for the data. This, however, is not quite the case, because the implications of these two positions are entirely different. Exploration implies that more novel stimuli elicit approach responses, whereas stimulus satiation implies that less novel stimuli elicit avoidance responses. These differences can be reduced to the question of whether the rat's and presumably other higher animals' orientation to the environment is essentially positive or negative, a problem which is fundamental to the study of motivation. Because of the importance of this problem, it seems worthwhile to mention other relevant experiments.

Walker and his associates [55] exposed rats to a specified stimulus. Later, the animals were placed in a two-choice situation (T maze) where one of the choices led to further contact with a stimulus similar to that previously experienced. According to the stimulus-satiation concept, animals should have avoided the familiar stimulus and chosen the other maze arm. Furthermore, the strength of avoidance should have increased with longer durations of preexposure. These predictions were not borne out by the data. In fact, the results of a second study showed no influence of stimulus preexposure on the rats' behavior at the choice point, even when the animals were preexposed to the goal box itself.

These data reflect adversely on the applicability of the stimulus-satiation concept in accounting for spontaneous alternation. And, by the same token, they raise real questions concerning the role of relative novelty in explaining alternate choice behavior. One point should be emphasized: Neither of the experimental conditions in the aforesaid studies involved preexposing the rats to the stimuli immediately adjacent to the choice point, and in all probability it is the stimuli bordering the choice point of the maze which have the greatest influence on behavior in this particular test situation.

This hypothesis was tested by placing glass doors at the entrance to each maze arm so that the experimental subjects could view the arms but could not enter them [37]. Both maze arms were painted either black or white, and rats were exposed to these stimuli for 1, 15, and 30 minutes. After the preexposure period, the animals were taken out of the maze, the glass partitions were removed, and a maze arm of the opposite color was substituted for one of the original arms. The rats were then returned to the maze, and the experimenter observed whether the animals turned into the newly inserted arm or into the one that had been present during the preexposure period. The data clearly showed that rats, following preexposure periods of 15 and 30 minutes, chose the new maze arm. A 1-minute exposure, on the other hand, had no effect on performance. This short preexposure should have affected the performance, however, if stimulus satiation is indeed the basis for spontaneous alternation in the rat. Usually, rats are exposed to the maze arm of their choice for only a few seconds, but this is sufficient time for producing alternate behavior. Perhaps a stimulus satiation concept is not applicable even to this study, where positive results were achieved with the longer preexposure conditions.

That a novelty factor eliciting exploration is a more suitable explanation is evident from a study by Dember [22]. He followed the same procedure as that described for the last study with the exception that one maze arm was white and the other black during the preexposure period. The duration of preexposure was 15 minutes. On the formal test trial, one maze arm was changed so that both were the same color. Since both maze arms were now identical and rats were equally satiated to the color of each, it would be reasonable to expect that half of the rats would enter one arm and half would enter the other. But this did not occur. Rats chose the arm that was newly inserted. This finding supports the thesis that an exploratory motive underlies spontaneous alternation and, more generally, that the behavior of rats in these kinds of situations is basically that of approaching instead of avoiding the environmental stimuli.

Influence of Novel Objects. Although the renewed interest in exploratory behavior stems largely from observations on the rat's behavior in the T maze, more ways of studying this phenomenon are available. If novelty is the basis for exploratory behavior, why not just place novel objects in the animal's environment and watch the animal's reactions to these objects?

This simple and straightforward technique of investigating exploration was first introduced by Berlyne [4]. He exposed animals to familiar and unfamiliar objects. The amount of exploration, as measured by time spent sniffing at each object, was recorded, and the outcome was in accordance with the "novelty" hypothesis. Rats explored the new or unfamiliar object significantly more than they did the others. In a more detailed study, where the number of approaches to a single object was recorded automatically, Berlyne [5] was able to show that the greatest amount of exploratory behavior occurs within the first minute of object exposure. Further exposure to the same object results in a steady decline in exploration. This demonstration of rapid satiation to a single object strengthens the argument that novelty is an important factor for exploratory behavior.

Using Berlyne's technique, Thompson and Solomon [53] demonstrated pattern discrimination (vertical striations versus an inverted isosceles triangle) by the rat by simply making one of the patterns a novel stimulus. More specifically, an experimental group was exposed to the striations (test 1) and then to the triangle (test 2). A control group was presented with the triangle for two successive tests. The results showed that the experimental group spent more time exploring the triangle (test 2) on the second test than did the control group. Had not the patterns appeared different to the animals in the experimental group, they would not have reacted to the triangle as if it were a novel stimulus.

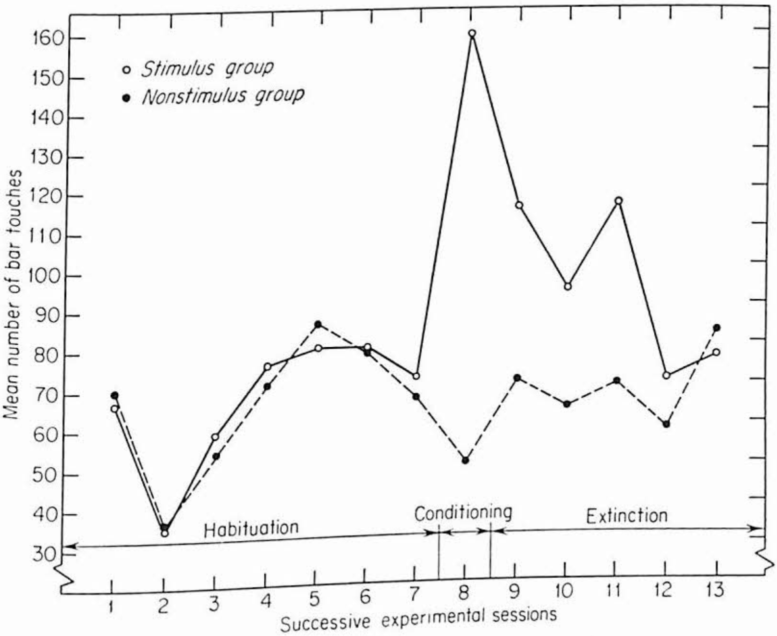

Fig. 6-6. The reinforcing effect of onset of illumination on bar-pressing responses. [*From G. B. Kish, Learning when the onset of illumination is used as a reinforcing stimulus. J. Comp. Physiol. Psychol.*, 1955, **48**, 261–264.]

Learning Studies. The next group of experiments to be discussed follows the paradigm of conventional learning experiments. Instead, however, of using food to reward the animal for responding in a specified way, the reward consists of a change in the environmental stimuli. Some investigators have used changes in illumination level as a reward. For example, Kish [36] placed mice in a darkened box for several daily sessions and recorded the frequency of operant lever pressing. The animals were then divided into two groups, referred to in Figure 6-6 as the stimulus group and the nonstimulus group. These groups were matched with respect to the number of lever presses emitted during the early or habituation phase of the study. On the eighth test day, the animals in the stimulus group were reinforced by onset of light each time they pressed the lever; those in the nonstimulus group were never rewarded by light for lever pressing. Figure 6-6 indicates that when light was used as a reinforcer, the mean number of bar touches by the stimulus group increased markedly over that recorded for the other group. The figure also shows that when the light reinforcement was withdrawn on subsequent test sessions, the number of bar touches emitted by the stimulus group eventually decreased to that level exhibited during the habituation phase of the study. Comparable results, using light as a reinforcer, have been reported where rats served as the experimental subjects [23, 40].

In the same line, Montgomery and Segall [47] made the opportunity to explore a complex maze contingent upon a correct response to a black-white visual-discrimination problem. Rats were run in a T maze with one arm of the maze painted black and the other white. The arms could be interchanged so that sometimes the black arm was on the left of the choice point and at other times it was on the right. Half of the animals were reinforced for choosing the black arm and the other half for choosing the white arm. Reinforcement consisted of being allowed to explore another, and more complicated, maze. Incorrect responses were followed by a 15-second confinement in the arm of the maze that the rat entered. All animals learned the discrimination problem, performing at a relatively proficient level.

An extremely provocative experiment in the area of exploration motivation was conducted by Myers and Miller [49], although these investigators, at first, intended to study a different phenomenon. Miller, as you recall, did the classic experiment on the drive properties of learned fear. Using the same apparatus as that employed in the fear study, an attempt was made to find out whether a learned drive could be demonstrated when hunger rather than escape from pain was the primary drive. The importance of this problem was considered in the section "Acquired Approach Drives." To recapitulate briefly, if learned drives can be established only through painful or anxiety-producing situations, then the applicability of this concept is severely limited. By showing that a drive can be acquired on the basis of a positive rewarding experience, in this case the attainment of food by hungry rats, the usefulness of the learned drive as an explanatory concept for man's behavior would be greatly augmented.

The procedure followed in this study was that of training rats on a door-pressing response for food reward. Rats were placed in one of two compartments separated by a door. The door dropped each time a rat touched it, thereby allowing the animal to enter the adjoining compartment, where it found food. One group of subjects received seventy food-rewarded trials, another group was given thirty trials, and the third group received ten trials. After acquisition of the door-touching response, the animals were again placed in the apparatus. This time, however, they were satiated with food and water, and no food was present in the adjacent compartment. Pressing a bar instead of touching the door now activated the door-opening mechanism. The bar, incidentally, had been present during the training trials. All three of the groups learned the new response without further food reinforcement, and it appeared that an acquired approach drive based on hunger had been established.

But this is not the complete story. In the first place, animals that had received only ten acquisition trials learned as rapidly as did those that had had seventy acquisition trials. In other words, strength of the learned drive, as measured by response latency, was not dependent upon the number of previously reinforced responses—a finding that is inconsistent with the results of many other studies on learning. More important, however, was the fact that a control group, receiving no acquisition training, also learned to press the bar to attain entrance into the other compartment. Moreover, learning by the control group was as rapid as learning by the other groups. These results led Myers and Miller to postulate that an exploratory motive was responsible for the rats' performance.

They then conducted another experiment using a new group of rats. No hunger-reward training was given. Animals, surfeited for food and water, were put in the apparatus to see if they would learn the bar-pressing response merely for the opportunity to explore the other compartment. Positive results were attained and exploration was probably the motivational basis for learning.

Relation to Other Motivating Conditions. The studies considered thus far show that changes in external stimulation can activate an exploratory motive. Since there was no apparent biogenic drive operating in these experiments, the question arises whether exploration motivation is a primary motive in the sense that hunger and thirst are classified as being primary. Failure to find a learned drive based on hunger, while in the same situation obtaining evidence for an exploratory motive, suggests that exploration is not directly dependent upon the hunger drive and presumably not upon the thirst drive either. But does hunger in any way influence exploration? Adlerstein and Fehrer [1] found that food-deprived rats explored from 50 to 75 per cent more units of a complex maze than they did under the condition of food satiation. This finding can best be evaluated by considering the effect of food deprivation on activity. It is known that rats are more active when hungry than when satiated. Moreover, the activity of hungry rats is further increased when they are exposed to external stimuli as opposed to being kept in the dark [20, 26]. Adlerstein and Fehrer's subjects when hungry were simply more active, and since exploration was measured in terms of the number of maze units traversed, the food-deprived rats, by definition, showed a greater amount of exploration.

Since activity and exploration can be easily confounded, perhaps exploration is nothing more than an expression of an activity drive, which in turn is influenced by a variety of conditions. Evidence supporting the existence of an activity drive comes from studies showing that the amount of activity, as measured by performance in an activity wheel, is proportionate to the duration of enforced inactivity [33]. In addition, the opportunity to engage in running behavior can act as a reinforcer for bar-pressing responses [38]. Such a drive certainly can account for the locomotion of a rat through a maze containing no extrinsic reward, but it cannot account for the pattern of behavior. As was stated earlier, rats tend to go to those maze units least recently occupied. More direct evidence against explaining exploratory behavior in terms of an activity drive is available from one of Montgomery's [44] studies. Rats that were confined in small cages for several days, as well as rats that were given free access to an activity wheel during this same interval, showed approximately the same amount of maze exploration when tested at various times during the course of the experiment. The point here, of course, is that those rats that were denied activity privileges should have engaged in a greater amount of exploration, if exploration is merely the behavioral consequences of an activity drive.

Several writers have suggested that a tenuous division exists between fear and exploration. A novel stimulus may simultaneously evoke fear and the urge to investigate. An approach-avoidance conflict results which is eventually resolved in favor of the stronger of the two competing tendencies. Experimental data are in essential agreement with this point of view. Rats, for instance, are less inclined to run in an open, elevated maze than in one that is enclosed. Presumably, they are more fearful when placed out in the open. In one study, rats were housed in a small enclosed cage which had a vertically sliding door at one end [45]. After a while, the door was raised. One group of rats was exposed to an enclosed runway, while the other group was confronted with an elevated runway. The strength of the exploratory motive was measured in terms of the number of maze sections traversed. The strength of fear, on the other hand, was measured by the number of retreats to the rear of the cage and the frequency with which animals looked toward the adjacent alley, then looked away. On the first test day, the enclosed runway elicited more exploratory behavior, and the elevated runway evoked more fearful behavior. This difference persisted on subsequent tests, but the interesting finding was that within a test session exploration decreased for the enclosed-runway group and increased for the elevated-runway group. In other words, both exploration and fear decreased as a function of exposure time to the runways. In the case of the elevated runway, exploratory behavior was not evident until fear was reduced. Under conditions of strong fear, exploratory behavior can be completely suppressed [46].

Research with Monkeys

A set of motivational mechanisms similar to that described for rats appears to be more prominent in the monkey. Different testing techniques are required, since the behavioral manifestations of the curiosity-investigative motives are quite different for monkeys. Unlike the rat, monkeys are remarkably adept at examining objects through manipulation and persist in this activity for prolonged periods of time. There is little question that this propensity for manipulation serves to acquaint monkeys with a wide variety of things in their environment. Aside from the presence of highly developed manipulative abilities, monkeys make much greater use of visual and auditory stimuli in keeping abreast of events occurring in their surroundings. This reliance on vision and audition is apparent even from the most casual of observations. Monkeys follow visually all activities in their vicinity and are extremely alert to environmental sounds. It is indeed difficult to escape the notion that these behavioral mechanisms are a direct expression of general exploratory motives, an idea which is more compelling in the light of experimental evidence. The evidence supporting this thesis is obtained from studies demonstrating that monkeys perform various tasks for no rewards other than those inherent in the process of manipulating, seeing, and hearing.

Manipulation. Harlow and his associates [29] carried out the first formal experiments on manipulatory behavior in monkeys. They argued that if manipulation has the status of a motive, then learning should be demonstrable without recourse to any rewards other than those inherent in manipulative activities. Rhesus monkeys were confronted with a three-part mechanical puzzle similar to that illustrated in Figure 6-7. Correct solution of the puzzle consisted of first lifting the pin, then moving the hook to one side, and finally raising the hasp. Touching any of the puzzle devices out of sequence constituted an error. Two groups of monkeys, experimental and control, were tested. For the experimental group, the puzzles were assembled and attached to their home cages, remaining there for several days. The subjects were permitted to manipulate the devices and the puzzles were periodically reassembled by the investigator. Those monkeys in the control group were treated differently, in that the puzzles were never assembled, thus preventing the animals from learning the correct solution to the puzzle. When both groups were later tested for puzzle solution, it was clearly evident that the experimental group had learned the task, whereas the control group committed many errors. A manipulation motive was postulated as being the most satisfactory explanation for the observed performances.

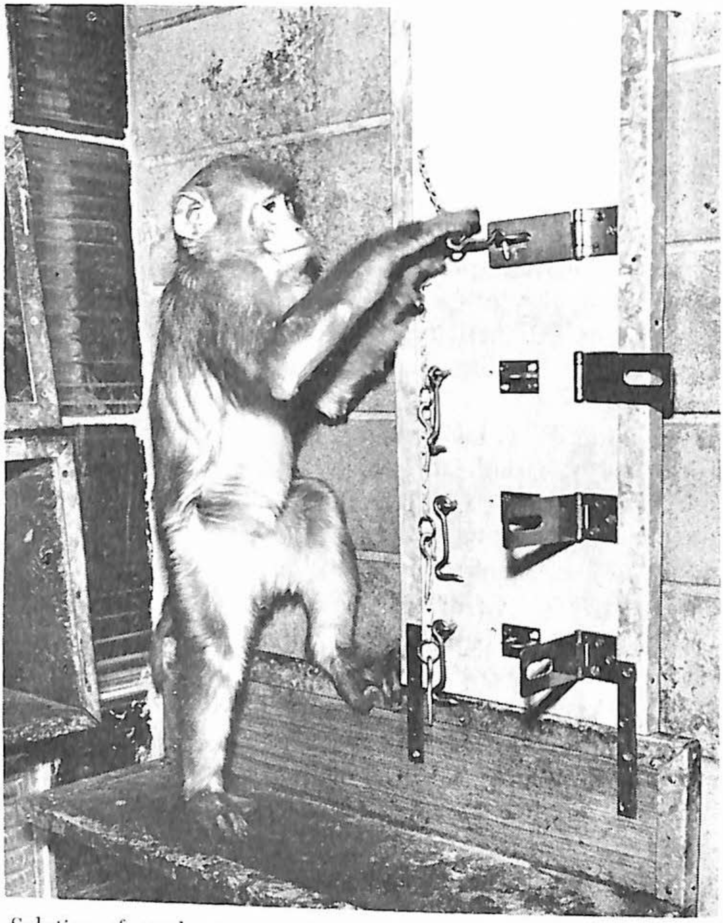

FIG. 6-7. Solution of mechanical puzzle in which pin, hook and eye, and hasp were disengaged in serial order. [*From H. F. Harlow, M. K. Harlow, and D. R. Meyer, Learning motivated by a manipulation drive. J. Exp. Psychol.*, 1950, **40,** 228–234. *Courtesy of Harry F. Harlow.*]

This experiment was repeated, using a more complicated puzzle consisting of six devices to be manipulated in strict serial order [27]. Again, animals were able to solve the puzzle without the introduction of other incentives, such as food, into the problem. More important than the demonstration of puzzle solution, however, was the finding that monkeys will perform on this problem for prolonged periods of time and still not become completely satiated with the task. For example, after the animals had learned the puzzle, the experimenter reset the puzzle every 6 minutes throughout the course of a 10-hour test session. Even under this condition, designed exclusively for satiating manipulative behavior, the monkeys continued to work on the problem for the entire period. Although there was a decrease in the actual number of devices manipulated as the session progressed, one or more devices were manipulated nearly every time the puzzle was reset. The persistence of manipulative behavior strongly suggests that manipulation is not a secondary motive conditioned upon some primary motive, but that it is in itself primary. That manipulative tendencies are exhibited by infant monkeys even before they have ever handled solid food lends further credence to the thesis that manipulation motivation is a primary behavioral determinant [28].

Realizing that puzzle solution is a somewhat atypical example of learning situations, Harlow and McClearn [30] went on to study the efficacy of manipulative rewards on a discrimination learning problem. The authors chose this kind of problem because it is basic to a wide variety of complex tasks investigated in the laboratory. A color-discrimination task was selected in which correct responses were rewarded by allowing monkeys to manipulate and examine the discriminanda. They were presented with a board containing five pairs of screw eyes (see Fig. 6-8). All of the screw eyes appeared to be securely fastened to the board, but one member of each pair could be easily removed. Those that were removable were colored differently from those that were fixed. A correct response was defined as touching or grasping a removable object, and an error was recorded when the animal touched a fixed object. The subjects were tested on seven different color-discrimination problems, with each problem consisting of four test sessions. The results showed a progressive improvement in performance, demonstrating that discrimination learning can occur when using manipulative incentives.

Visual Exploration. In cognizance of the fact that monkeys spend many of their waking hours merely watching events taking place in the vicinity, a series of experiments has been conducted in which the opportunity to explore visually is used in motivating animals to perform certain tasks. The apparatus employed in visual exploratory studies was simply an enclosed box with a small door which could be opened by the animals. Since, by convention, the process of learning implies the presence of a motivating condition, the first problem investigated was that of discrimination learning [12]. In this experiment, the enclosed box contained two small doors. Differently colored cards were inserted on the inside face of each door. Both doors were closed, but one was always unlocked while the other was always locked. The color of the card attached to the particular door served as the cue for determining whether the door was locked or unlocked. In one instance, a yellow card was fixed to the unlocked door, and a blue card was fastened to the locked door. The cards were frequently switched from door to door, thus ensuring that color of the card rather than position of the door was the critical cue for problem solution. If the monkey pushed against the card on the unlocked door, the door opened, and the animal was allowed 30 seconds to view the situation outside the box. A monkey just completing a correct response is shown in Figure 6-9. The view, incidentally, was the entrance room of the laboratory, where several people usually congregated. If the monkey happened to push against the card on the locked door, his efforts went unrewarded, since he could not look outside the box.

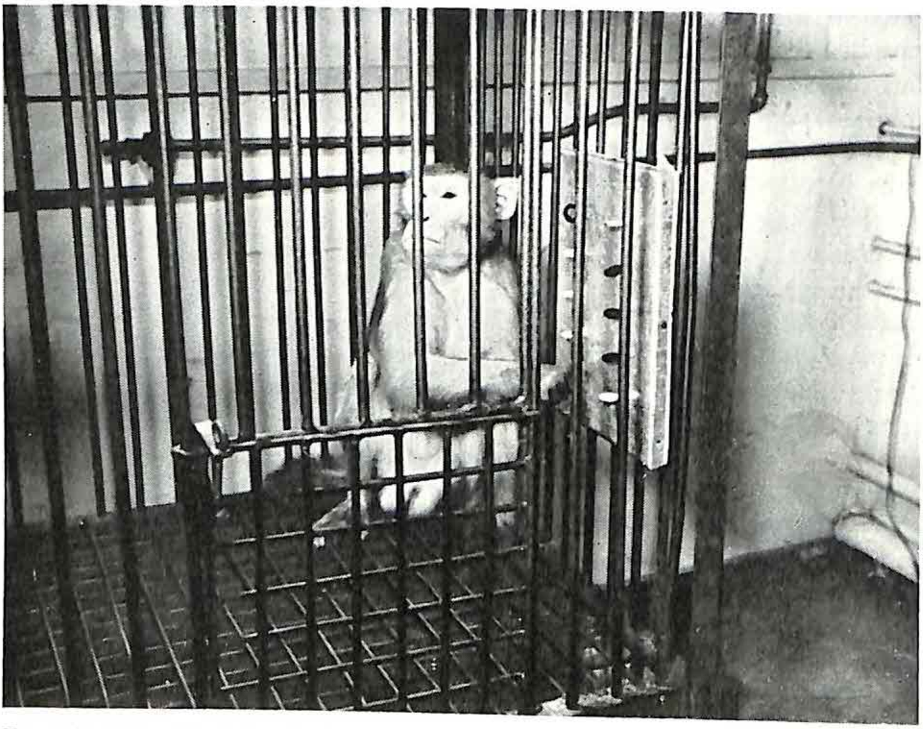

FIG. 6-8. Color-discrimination learning to manipulative incentives. [*From H. F. Harlow and G. E. McClearn, Object discrimination learned by monkeys on the basis of manipulation motives. J. Comp. Physiol. Psychol.*, 1954, **47,** 73–76. *Courtesy of Harry F. Harlow.*]

The outcome of the experiment was quite clear. Monkeys learned the color-discrimination problem for visual reward. Repetition of this study with other monkeys being tested on several color-discrimination problems yielded similar results [19].

The data on the persistence of visual exploratory behavior are of enormous theoretical interest. Rhesus monkeys, when tested until they failed to push against either door within a 10-minute period, performed for many continuous hours [18]. In fact, one animal worked for nearly 20 hours before it finally refused to respond to visual incentives. To obtain more direct information on the strength of visual exploration motivation, another study was carried out which did not incorporate a discrimination-learning task into the experimental design [17]. This time, monkeys were tested in a box containing only one door. The door was held closed by a spring, but it could be opened easily by the subjects. The reward for opening the door was a view of a monkey colony. As soon as the monkeys released the door, it closed abruptly. Animals were tested 10 continuous hours a day for six consecutive days. The number of door openings and the length of time the door was held open were recorded automatically.

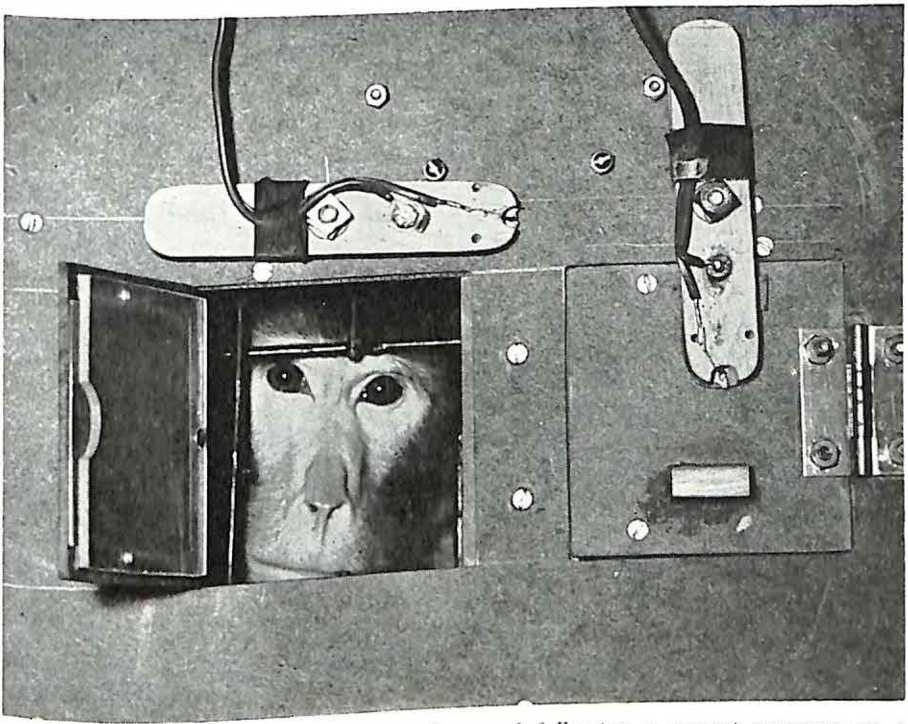

FIG. 6-9. A monkey partaking in visual reward following a correct response on a color-discrimination problem. [*From R. A. Butler, Discrimination learning by rhesus monkeys to visual-exploration motivation. J. Comp. Physiol. Psychol.*, 1953, **46,** 95–98.]

As in the previous experiment, the results testified to the motivational strength of visual exploration. Total time spent viewing the monkey colony was relatively constant from day to day, averaging 40 per cent of the testing period, which ran 60 hours for each subject. These data strongly indicate that visual exploration is not based on primary biological drives, because, if it were, satiation to visual incentives should eventually occur when no extrinsic reinforcement is provided.

The degree of responsiveness to visual incentives depends upon the class of visual stimuli employed [13]. It seems appropriate to spend some time on this point, since the possibility exists that monkeys may push open a door for manipulative incentives only, with visual events occurring outside the box having a minimum effect on performance. When animals are observed working in this type of situation, there is little doubt that visual incentives are primarily responsible for the maintenance of a high level of motivation. Nevertheless, systematic observations are more compelling than casual observations, and the following experiment was carried out to discover the influence of different visual incentives on visual exploratory behavior.

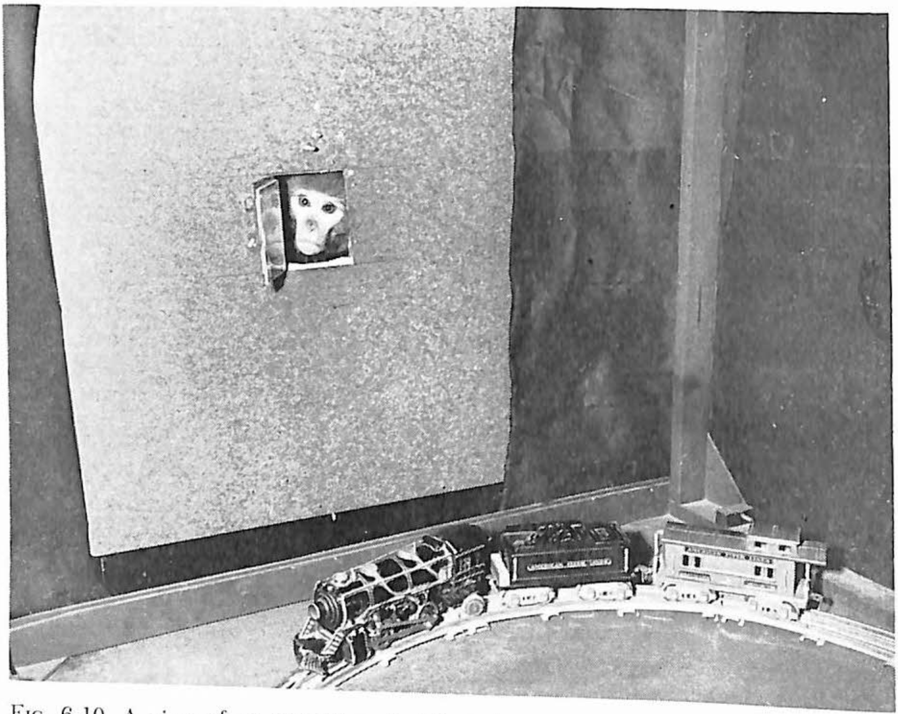

FIG. 6-10. A view of an operating electric train serves as the monkey's reward for pushing open the door. [*From R. A. Butler, Incentive conditions which influence visual exploration. J. Exp. Psychol.*, 1954, **48,** 19–23.]

Monkeys, upon pushing open the door, could view a rather large enclosed chamber. On some tests, the chamber was empty, but on other tests it contained either another monkey, an operating electric train, or an array of food highly palatable to monkeys. Each time the subject opened the door, it was allowed 5 seconds to view the chamber and its contents. Figure 6-10 shows a monkey at the door when an electric train occupied the chamber. Most responses were made when another monkey served as the visual incentive. Next in order of incentive value was the electric train, then food, and last, the empty chamber. The fact that the electric train elicited many more responses than did the food is significant, since food was undoubtedly a strong secondary reinforcing stimulus and the monkeys had probably never seen anything comparable to the train. The monkeys still opened the door when the chamber was empty, which suggests that manipulation was playing some part in maintaining performance. It should be mentioned, however, that the chamber, even when devoid of other incentives, still provided an expansion of the subject's visual field.

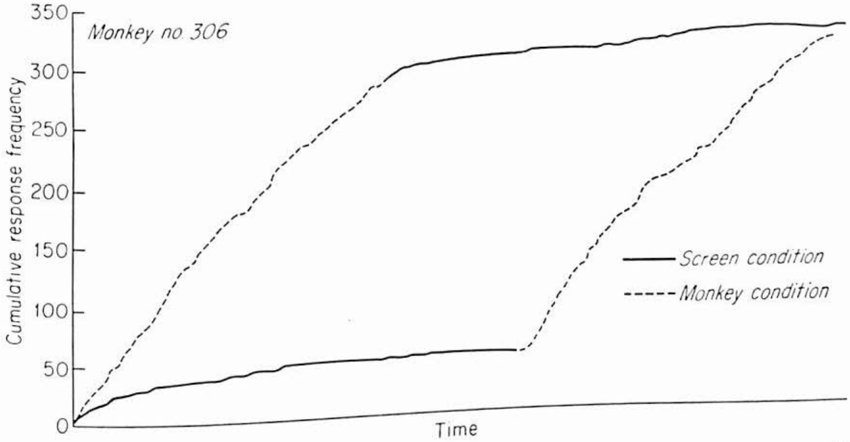

FIG. 6-11. An example of the effect of different visual incentives on response rate. The recording pen was made inoperative during intervals of visual reward.

There was no evidence indicating that the animals were satiating on any of the experimental conditions, but satiation to a visual incentive could be shown when the stimulus was stationary and homogeneous. Figure 6-11 illustrates this point by showing the rate of door-opening responses when a monkey was rewarded with a view of a homogeneous white screen. The response rate for a view of another monkey is included in this figure to reemphasize the differential influence of contrasting incentive conditions on behavior. In this instance the monkey was given two tests, each of which lasted for 60 minutes, with 30 minutes being allotted each incentive condition. Other animals behaved similarly, but the difference in responsiveness between these two visual-incentive conditions was not as dramatic.

The underlying factor in all of the studies on visual exploration is that of stimulus change. The monkey has the opportunity to view a different stimulus configuration by opening the door. Some configurations elicit more responses than others. Studies on mice and rats, discussed earlier, indicate that stimulus change in the form of increased illumination level can reinforce lever-pressing responses. Here there is no concomitant change in the visual scene following a response. The same phenomenon has also been reported for the monkey, with the interesting finding that both increases and decreases in illumination level elevated the frequency of lever-pressing responses over that recorded for a control group [48]. Since each subject was given only one 60-minute test, no information on satiation is available. It is unlikely that the responsiveness of monkeys to stimulus change would persist if the stimulus configuration did not vary periodically.

Since fear appears to be the antithesis of exploration, Butler [16] investigated the effect of a fear-producing situation on the visual exploratory behavior of the rhesus monkey. Briefly, the subjects, upon opening the door of the box, were exposed to a cage which contained either a large dog or another monkey. A control condition was an empty cage. Each animal was tested 30 minutes on each condition.

Only one monkey in the group of five opened the door when the dog was used as the incentive, and this subject responded just once. The barking of the dog, in addition to the fright sounds of other monkeys, presumably produced a state of fear which served to suppress exploratory behavior. Number of responses when another monkey was in the cage was considerably greater than response frequency for the control condition. Had the monkeys been tested repeatedly with the dog as the incentive, they might have commenced responding eventually. Montgomery's [45] rats, for example, started exploring the elevated maze after their initial reluctance to enter the runway.

There are, in all probability, many ways to influence the amount of visual exploratory behavior, with changes in the visual-incentive conditions being only one of the more obvious techniques. Preliminary results suggest that brain damage can affect visual exploration, particularly when the lesion is located in the temporal lobes [18]. Another technique that can effectively modify visual exploratory behavior is deprivation, but in this instance "deprivation" refers to the lack of opportunity to look outside the enclosed box for several hours. Illustrating this point is a study where the responsiveness of rhesus monkeys to visual incentives was tested after 0, 2, 4, and 8 hours of confinement in the box [14]. The test itself lasted for 1 hour, and response frequency to the single door served as the indicator of motivational strength of visual exploration. A monkey colony provided the visual incentives.

Not unlike the results in the hunger-food studies, the rate of response was positively related to the duration of deprivation. Response rate on the test given after 8 hours of deprivation, however, was not appreciably greater than that recorded following the 4-hour deprivation period. In part, these results reflect the functional similarities and differences between behavior motivated by hunger and behavior motivated by visual exploration. In both cases, the responsiveness of the animals increases with increased durations of deprivation. But with visual exploration, the effect of deprivation appears to reach a maximum after only 4 hours.

Auditory Exploration. Monkeys are highly visual animals, in that vision is of tremendous importance for orienting them to their surroundings. At the same time, hearing undoubtedly plays a commanding role in the monkey's interaction with the environment. The question arises whether monkeys will perform for auditory rewards in a manner comparable to that observed when vision serves as the reinforcement, and the data available on this issue indicates that they will.

Rhesus monkeys were tested in a sound-treated booth located in a room adjacent to one housing a monkey colony [15]. A microphone and an amplifier, placed in front of the colony, were connected to a loudspeaker which was fastened to the top of the test cage. Inside the test cage were two levers fixed to opposite walls. Pressing one of the levers was followed by sounds emitted from the colony. No sound reward was given when the other lever was pressed.

The results showed convincingly that monkeys selected the lever which provided sound reinforcement more frequently than they did the control lever. When the auditory reward was switched to the opposite lever, the performances of the animals were modified accordingly, in that responses decreased to the original lever and increased to the lever that was now rewarded by sound. Although the frequency of responses to each lever was differentially influenced by sound reward, there was no decrease in total number of responses throughout a series of 20 test sessions. Instead, total response frequency increased as the experiment progressed. These results strongly suggest that auditory exploration is similar to other exploration motives, for it can be maintained at a high level without introducing other kinds of rewards. A subsequent study has shown that monkeys will consistently press a lever more frequently to hear some sounds than they will to hear others. For example, the sound of a monkey calling to its cage mate has a much greater incentive value than the sounds of an enraged monkey colony or the sound of a barking dog [16].

Research with Chimpanzees

Little formal experimentation has been done on the exploratory behavior of the chimpanzee. This is indeed regrettable, since a study of the genesis of exploration in chimpanzees should provide invaluable information for more clearly assessing the role of the curiosity-investigative motives in the behavior of man. The data that have been accumulated, however, certainly go along with results obtained on lower animals and also agree with observations on the behavior of young children. Welker [56] investigated the chimpanzee's reactions to novel stimuli. His testing technique consisted of recording the animal's behavior when a pair of stimulus objects was placed just outside its cage. Each member of the pair differed from the other with respect to one or two characteristics, such as size, form, color, brightness, texture, and movability. Each set of objects differed markedly from the other sets. The number of times that the subjects either manipulated the objects or looked toward them was recorded on a time-ruled data sheet. Every pair was presented for 6 minutes daily until the responsiveness of the chimpanzees decreased to a relatively stable level. Another pair was then introduced. After the animals again reached an asymptote of satiation, the objects were discarded and a third pair was made available. This procedure continued until all animals had been tested on fifteen different pairs of objects.

As might be expected from the description of the study, animals became satiated after a few test sessions with the same objects. Manipulation, accompanied by close examination, however, could be elicited again with the introduction of new sets of stimuli. Further investigation showed that a group of heterogeneous objects evoked many more responses than did a group of objects that were alike [57]. In the former situation, the chimpanzees' behavior was not unlike that of young children. They reached for one object and then another in relatively rapid succession. Each member of the heterogeneous group possessed a greater degree of novelty; hence, exploratory behavior was sustained at a high level.

Welker's experiments also demonstrated that young chimpanzees (three to four years) were more responsive to objects than the older animals (seven to eight years). Conversely, chimpanzees in their first or second year exhibited a marked degree of timidity when novel objects were placed before them [58]. After a few minutes, these youngest animals began to reach for the objects and to play with them. When other new objects were introduced, the infants again withdrew and watched for a while before making manual contact with the stimuli. Welker believed that the greater variety of experience with objects on the part of the animals three years of age and older eliminated fear for the new and different objects. In this connection, Hebb and Riesen's [32] work on the reactions of chimpanzees to strange persons is relevant. Animals less than two years old feared and avoided strangers even after several exposures, whereas the older chimpanzees adapted more readily to their presence.

Research with Children

Young children should be excellent subjects for research on the curiosity-investigative motives. They engage in a great deal of manipulatory behavior and are extremely responsive to different visual and auditory stimuli. It is entirely conceivable that the curiosity-investigative motives are largely responsible for the child's early and extensive learning of environmental events and their interrelations. Research in this area has hardly begun, even though there is little question that the motivational basis for the behavior of children is one of the most important problems in psychology.

Berlyne [6] has demonstrated systematically that children will perform on a simple task for visual rewards. He found them much more responsive than adults under these testing conditions. The maintenance of play behavior by nursery school children has been studied by Hayes [31]. Children were invited to play simple games, such as dropping marbles through a slot and retrieving them at a tray in the bottom of the apparatus or pressing a lever that produced noise. Although the subjects would become satiated with any one game, changing games served to reinstate play behavior to its original level—a finding similar to that reported for chimpanzees.

The results of all studies on curiosity-investigative motives indicate that the responsiveness of the organism is highly dependent upon a diverse and changing external environment. It is important to mention here that severe restriction of environmental stimuli during infancy can markedly retard a child's development [52]. Even with adults, sensory deprivation can produce distressing psychological effects which frequently happen within a few hours [7, 39].

SUMMARY

The experiments described in this chapter reflect a new and growing interest on the part of comparative psychologists in extending the study of motivation far beyond the confines of the primary biological drives. One main contribution toward this end has been the demonstration that drives can be acquired which impel the animal to avoid certain fear-provoking situations. The other has been the accumulation of evidence strongly suggesting that something akin to curiosity exerts a powerful influence on the behavior of animals. Both lines of investigation have direct implications for man's behavior and, in conjunction with the biological drives, provide a broad research-oriented foundation for a comprehensive theory of motivation.

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CHAPTER 7

Learning

Learning is a process which occurs as a consequence of stimulation or of behavior and results in a change in the behavior of the organism. To qualify as evidence for learning the change in behavior must be redintegrative. This means that a new or a more consistent association between environment and the organism's reaction to it is revealed. There is a demonstrable increase in the efficacy with which cues may control responses.

Cond

Learning is measurable only after it has occurred. A change in the response to a stimulus is measured directly on any trial or trials after the learning has occurred by a measurement or qualitative observation applied to that response. A change in stimulus-stimulus associations can only be indirectly inferred on the basis of its subsequent behavioral effects. Psychologists have much to learn about such integrations between stimuli, for they are only beginning to find techniques for uncovering them. They know equally little about response-response integrations, which contribute to the development of learned skills. The study of motor skills in animals has received relatively little experimental attention. Phylogenetic advances are most impressive in perceptual and motor-skill types of adaptation. Stimulus-response modifications and the laws governing their production are remarkably similar wherever they are found in animal behavior.

Learning is distinguished from other classes of behavioral change. Temporary change in behavior, quite distinct from learning, may result from recurring fluctuations in motivation, fatigue of the responding musculature, injury, or illness. Any maturational process in which growth is independent of the effects of stimulation or practice may sometimes be confused with effects of learning. Comparative psychologists study all such significant factors by measuring their behavioral consequences; instead, in the present chapter we shall examine the conditions and events that produce learning in various representative animals.

CLASSIFICATION AND MEASUREMENT

Learned modifications of behavior are one of the more important biological phenomena in the over-all process of organismic survival. No simple categorization does justice to all varieties of the learning process found in animals. Modern theories of learning are grounded in studies of learning in animals, and they deal with the relationships between stimuli or cues on the one hand and responses or activities on the other. Somewhat subsidiary in most theories to the accounting for stimulus-response relations are concepts dealing with (*a*) changing associations between one stimulus and another, which in this chapter will be called S→S learning, and (*b*) changes in response integrations, which will be called R→R learning. While the pure case of R→R learning may be difficult to find, the systematic and complete treatment of motor skills demands such a category.

Descriptions of Stimuli and Responses

Learning is often a function of stimuli from the external environment and can most easily be studied when it is, especially in animals. But much that we observe attests to the importance of internal stimuli. Behavior is controlled by kinesthetic and proprioceptive stimuli and by internal chemical states which act as stimuli or sensitize the organism to certain stimuli. Complex maze learning, learning where rewards are delayed, delayed response, and problem-solving behaviors are all dependent, among other factors, on various internal sources of stimulation. Drive states, for example, can serve as the sole differential cues for learned spatial discriminations [3], and until sensory processes have proprioceptive effects, they are virtually useless in either delayed-response or delayed-reward learning [15, 40].

In practice we may find one source of stimuli easier to control than another, but for purposes of categorizing learning processes we do not completely separate the external from the internal or the physical from the social or biological environments. There is no sharp dividing line by which to isolate such environmental events, nor are there principles of learning which are unique to one or another of these categories. For purposes of general descriptions of behavior, including learned alterations seen in comparative studies, the different aspects of the environment emphasized by concepts of this kind are sometimes useful. Their arbitrariness, however, must not be forgotten.

Responses are also separated into overt and covert, skeletal and autonomic, mechanical and linguistic, to mention several that are neither quite parallel nor quite independent. As so often happens in biological science, the either-or classification breaks down upon close examination. So we find that methods and instruments for measuring responses vary from the easy and obvious to the technically difficult and highly abstract. The measure of behavioral change used in an experiment usually represents some concession to expediency. Complete description is impractical if not impossible. The animal experimenter selects an aspect of behavior which is unambiguous, such as direction of locomotion, movement of a limb, or pressing of a bar. These indicators give "objective" and quantifiable data. They never represent all that is in process of change. This means that any single measure of degree of training as reported simply in numbers of trials or of right and wrong responses is not a complete account of learning effects. Multiplicity of measures is now used with increasing effectiveness by some experimenters. There is need for further development of recording techniques and for efficient methods of synthesizing data as results are obtained from various recording devices operating simultaneously.

The Duration of Learning

Learning processes result in relatively long-lasting behavioral changes. How long they last must vary with the animal being studied. We are faced here with an example of that general problem in comparative psychology: how do we obtain units of measurement (for time or for behavior) which are equivalent from one organism to the next? This is sometimes solved for time units by reducing them to equivalent subdivisions of the life span. Thus, if a chimpanzee shows retention from the age of four years to the age of eight, this would be closely comparable to the retention of human learning from the age of six years to twelve. There is evidence that each of these primates is capable of retaining learned behavior for somewhat longer than this. In simpler organisms a comparable time span might be a matter of only a few days or weeks.

Surprisingly few comparative studies have dealt satisfactorily with the problem of how long learning persists. Experimenters have rarely attacked this problem directly. They usually find it difficult to exclude interference or positive transfer from new learning when the animal is away from the experiment. Where, by careful control of living conditions, interfering experience is excluded, learning is remarkably durable. Insects are reported to retain visual-discrimination habits for several days and odor discriminations for several weeks. Visual-discrimination habits in birds are variously reported to last for one, four, or even six years [48]. Theoretical discussions in a number of contexts include the supposition that the effects of learning may persist for the life of the individual.

GENERAL PROBLEMS AND PARTIAL ANSWERS IN ANIMAL LEARNING EXPERIMENTS

Neither morphology nor biochemistry can yet tell the biologist where learning should first appear in the taxonomic series. The problem is answered only at the behavioral level of observation. Some discussions of that primitive kind of modifiability known as *habituation* include evidence in plants for this gradual reduction of response to stimulation [22]. Early attempts to study learning in animals employed tasks which demanded more than a single kind of learning. One trend has been toward simplification of methods for purposes of discovering the rudiments of each kind. This effort is partially successful, as will be evident in a later section of this chapter. But there are other questions which only complex tasks and longitudinal studies of animal learning can answer. To supplement the laboratory studies, many more naturalistic observations are needed for the broad exploration of the learning capacities of animals.

Maze Learning in Annelids

R. M. Yerkes in 1912 reported a study of learning in worms. His findings have been verified and extended. The not-so-simple properties of worm behavior at a right versus left choice point (Fig. 7-1) are worthy of study because they represent in a simpler organism, whose "brain" can be exchanged for a new one, several kinds of modifiability that persist throughout higher levels of the animal phyla.

The earthworm in a T maze is typically driven from its starting point by light, punished for a wrong turn by shock, and rewarded for the "correct" choice by permitting it to reach darkness and moisture. Depending on the criteria or measures of learning and the particular conditions of the experiment, worms learn in some 20 to 150 trials to turn consistently in one direction at the choice point [2, 21]. In about the same number of trials, worms have learned to abandon one direction of turning and adopt the opposite turn.

Experimenters have reported effects of prior familiarization and adaptation to the maze, species differences in avoidance and approach phases of learning, and the isolation of two or more stages in the development of consistent responses. Worms in T mazes exhibit an early phase of learning characterized chiefly by *avoidance* responses and distinguishable from a later phase involving increase in speed and directness of locomotion to the "goal." Annelids of two species tested in the same set of mazes [44] differ in the degree of specificity of their hesitating and backing responses to local cues within the maze. In the early phase, *Lumbricus terrestris* gives avoidance responses throughout the maze, whereas with *Eisenia foetida,* such responses seem to be confined to cues in the wrong alley. Whether this represents a difference in sensory capacity or in a motivational susceptibility to generalized avoidance conditioning is not clear. The average total numbers of trials required by animals of each species to reach a criterion of ten consecutive correct turns are approximately the same.

A good start has been made on the problem of what neural centers participate in earthworm learning [21, 59]. Anterior segments of the worm can be cut off without disruption of the maze habit. Segmental ganglia and the ventral chainlike nervous system clearly participate in retention. When the anterior segments and the normally dominant cephalic ganglion regenerate, the learned behavior disappears. It will require further research to determine whether this loss is complete, in the form of some neural alterations in each segment, or whether an inhibitory process prevents the behavior from occurring.

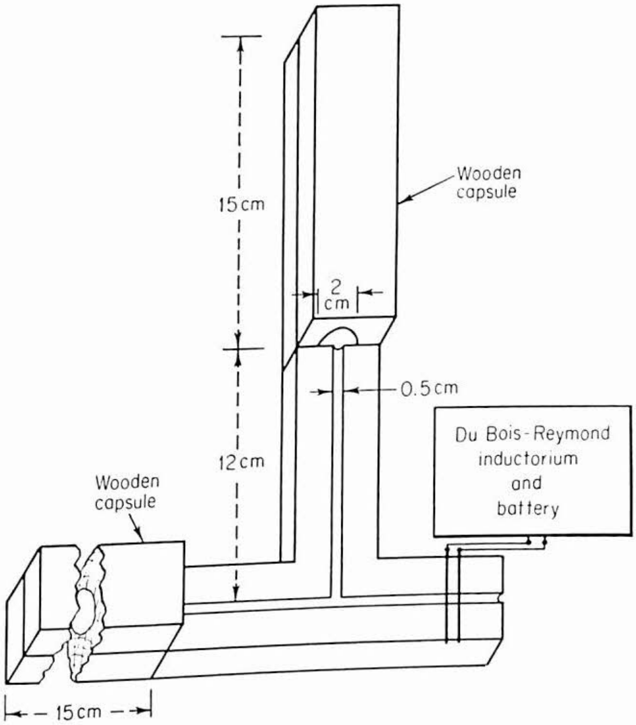

FIG. 7-1. A maze used for the study of spatial learning in earthworms. [*From L. Heck, Über die Bildung einer Assoziation beim Regenwurm auf Grund von Dressurversuchen. Lotos Naturwiss.* Z, 1920, **68,** 168–188.]

Earthworms require only about half as many trials to learn the correct turn in the maze if they are permitted to live and crawl about in the maze for a time before reward and punishment are introduced [2]. This kind of nonreinforced learning, studied extensively in experiments with rats, is usually called *latent* learning. Those theorists who hold that all learning requires gradually accumulating effects of reinforcement find it difficult to account for this kind of "savings" in trials. Others regard this as evidence for a strictly associationistic sensory learning mechanism, whereby the effects of the various stimuli occurring together or in sequence as the animal moves through the maze become associated with each other. These stimulus patterns become integrated into larger perceptual units to which responses may be more promptly attached. A third point of view places all the emphasis on the ability of organisms to attain perceptual units (gestalts) immediately after exposure to the entire problem situation. This last theoretical position would predict a cumulative improvement in performance only where the organism is exposed to a problem in a fragmentary manner. The very nature of a maze problem fits this description. Even so, it is difficult to apply the theory of perceptual gestalts to maze learning without some integrative principle like that of sensory-sensory association, which provides the mortar for cementing the bricks together. Once the parts of a maze can be discriminated as belonging to certain aspects of the whole, appropriate responses can be made by the organism at each discriminated choice point.

Avoidance Conditioning in Arthropods and Vertebrates

Animal psychologists recognize the maze problem to be a highly complicated one. They have spent considerable effort in the investigation of sensory cues that are required for learning and in studying the nature of the adaptations that are demonstrated in various mazes by the laboratory rat [25, Chap. 17; 31]. A somewhat unusual feature of the Yerkes T maze as used with worms is the arrangement for delivering shock for a wrong turn, but many other kinds of apparatus have used shock to produce discriminative responding. Monkeys have been trained in form, color, and positional discriminations by the method of giving shock for wrong responses and reward for right responses. In using shock an experimenter must always guard against the use of such painful intensities as may produce an avoidance that generalizes to the entire experimental apparatus. Emotional responses and generalized avoidance can be minimized by the use of moderate shock and by the use of a number of techniques which favor discrimination by the animal of the exact source and timing of the shock.

Avoidance conditioning is a special category of the more general class known as instrumental learning. In a typical avoidance-conditioning procedure a stimulus or a stimulus constellation from the environment precedes some "punishing" stimulus which in turn gives rise to a response or a complex series of responses. As a consequence of these responses the noxious stimulation ceases. The behavior is instrumental in terminating injurious stimulation on early trials but soon occurs as a response to the conditioned stimuli in advance of actual "punishment," whence comes the name instrumental avoidance conditioning. Whereas the criterion of learning is conveniently couched in terms of successful avoidance responses, autonomic reactions are seen increasingly to precede the noxious stimulus during the escape phase of learning. These autonomic reactions are evidence for the learned arousal of fear. Such conditioned fear may be regarded as distinct from the instrumental learning and is an example of classical (or respondent) conditioning. Ingenious methods enable an experimenter to record the acquisition of emotional behavior. Otis, Cerf, and Thomas [37] have recently developed recording tech-

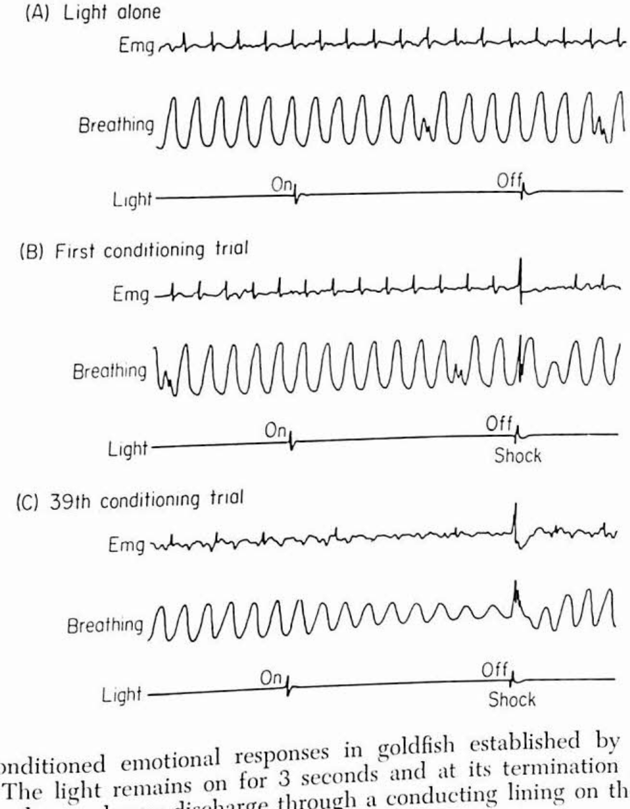

FIG. 7-2. Conditioned emotional responses in goldfish established by pairing light with shock. The light remains on for 3 seconds and at its termination a momentary shock is given by condenser discharge through a conducting lining on the sides of the small tank. Conditioning occurs in fifteen to forty trials. It shows up as reduced breathing (gill movements) and heart action in response to the light. [*Records by courtesy of L. S. Otis, J. Cerf, and G. J. Thomas, Conditioned inhibition of respiration and heart rate in the goldfish. Science*, 1957, **126,** 263-264.]

niques for heart rate and breathing changes in fish and applied these in a conditioning procedure (Fig. 7-2). Conditioned fear has important theoretical significance in accounting for long-lasting avoidance behavior and even in the learning of new responses without use of any noxious stimulus or other primary reinforcement.

Many laboratory studies of avoidance conditioning have been done with the cockroach *Periplaneta americana* or related species and with the white rat. A standard procedure is to use darkness, which normally elicits approach in cockroaches, as the conditioned stimulus for the avoidance of shock. The animals are permitted to crawl along a lighted alley, and when they enter a dark compartment, they receive shock through a brass grid on the floor of the compartment. Animals show considerable variability in the number of trials required before they consistently turn back after initially approaching the darkness, but on the average, 15 to 20 trials suffice to produce 9 correct responses in 10 trials [29]. Rest following such performance permits retention of the conditioned avoidance for several hours, whereas forced activity for 10 minutes immediately after learning interferes with retention, presumably by its effect on a "consolidation" process in the nervous system. When a sleeplike state is induced, there is sufficient retention for 24 hours to give a 75 per cent saving in the average number of trials required for relearning. Animals normally active during this time show less than 30 per cent saving.

Laboratory rats learn conditioned-avoidance responses in approximately the same number of trials as do the cockroaches, when trained under a similar procedure [30]. They can then learn new avoiding responses under the influences of the *conditioned* stimulus [28], a process of learning by secondary reinforcement.

Learning to Learn: Evidence for Species Differences

Few differences between species in learning capacity are demonstrated by maze problems or avoidance conditioning when only the learning of the initial problem is considered. Such differences as appear are often found upon analysis to reflect differences in sensory or response powers rather than in modifiability. Higher organisms show their advanced stages of development in terms of increasingly complex and modifiable perceptual capacities, their learning of highly coordinated response skills, and their ability to shift response from one stimulus to another on the basis of a single trial. Tests of an animal's ability to "learn to learn" are usually called discrimination-reversal, learning-set, or one-trial learning experiments.

The Dutch comparative psychologist Buytendijk was apparently the first experimenter to report one-trial positional-discrimination reversals in animals [5]. His experiment grew in part out of previous American studies of transfer of training between mazes. Buytendijk trained rats to take one turn in a T maze until errors were eliminated. Then the correct turn was reversed for retraining and so on until five reversed habits were completed. On the fifth reversal, eight of ten rats made only the single error at the beginning of the reversal. The ability of the rat to relearn on the basis of one trial has since been confirmed and is now known to depend, among other things, upon the degree to which the initial habits in the series of reversals are practiced [9, 39].

The increasing facility shown by Buytendijk's animals for reversing their choices of alley is shown by the average-error scores for ten rats on the initial habit and five successive reversals: 8.1, 5.5, 5.5, 1.8, 1.7, 1.3. This represents an efficient development of a position-reversal *learning set*. There is no evidence that invertebrate organisms can "learn to learn" in the positional problem of the T maze or in any other kind of laboratory problem. A study by Thompson [51] of the sow bug *Armadillidium vulgare* was modeled after the one described above. Thompson found no statistically significant improvement in eight reversals. More comparative studies with this technique are needed. The efficiency with which some insects in foraging for food are able to orient themselves spatially does suggest that a suitable experiment will one day demonstrate that some arthropods are capable of learning to learn to the specific stimuli and under motivation most appropriate for their modes of adjustment. This kind of learning problem is one we shall examine further in a later section of this chapter.

TYPES OF BEHAVIORAL MODIFICATION

Habituation and Sensitization

Two primitive kinds of behavioral change are closely related to learning but are usually considered in a special category. They must be distinguished from innately determined susceptibility to fatigue and from the effects of temporary motivational states. Both habituation and sensitization depend on exposure of an organism to stimulation and show cumulative change as a function of numbers of repeated stimulus presentations. Both appear very early in the animal scale, or possibly even in plants, and are exhibited throughout all the higher phyla.

Habituation: A Universal Phenomenon. The Peckhams [36] reported a noteworthy observation on the behavior of spiders in volume 1 (1887) of the *Journal of Morphology*. They were testing the reactions of *Epeira* and *Cyclosa* to vibrating tuning forks. On early trials the animal subject responded by dropping from the web on its thread to a distance of a foot or more, where it would remain for a time before returning to the web. As habituation proceeded on successive trials the distance of flight and the delay before return were gradually reduced. One animal was tested daily for a month, and at the end of the series it remained on the web even on the initial trial of the day. Also called "negative adaptation," this process of habituation is characterized by a gradual reduction in response to successive occurrences of a given stimulus.

Habituation to mechanical stimulation has been reported for several species of protozoans [38]. In phylum Mollusca the relatively active cephalopods provide excellent examples of habituation. Snails from quiet bodies of water are easily disturbed by mechanical stimulation. This high degree of responsiveness may be selectively "adapted out" in the laboratory by a systematic program of exposure to stimuli [50]. Snails from turbulent waters show a reduced initial responsiveness. One is tempted to draw the analogy between these groups of snails and persons accustomed to sleeping in the city as opposed to those who have just moved in from the country. The process works in both directions, for farmyard sounds often disturb the visitor from town on his first nights in the country.

In higher organisms with specialized receptors, habituation is clearly not the same process as sensory adaptation, which involves the sense organ itself. Whether the behavioral phenomenon which we identify as habituation will be found to depend upon the same physiological process at different levels in the phylogenesis of the nervous system remains an interesting question but need not deter us from using the concept to identify this class of behavioral modification. Thorpe [54] treats habituation as a simple form of learning and discusses possible mechanisms underlying it.

Sensitization as Nonassociative "Conditioning." Repetition of stimulation may produce the opposite effect from that just described. Whether the result of a series of stimulations will be sensitization or habituation seems to be largely a function of the strength of stimuli used. When a series of intense stimuli is given, the responses to weaker stimuli of the same or other sensory modalities may increase in strength or may appear where they previously failed. Grether [14] and others have shown that experimental controls are necessary to distinguish true conditioned responses from sensitization effects. Conditioning results only from the pairing of neutral stimuli with effective stimuli or reinforcement. A comparable series of stimulations where the neutral and the effective stimuli are separated in time may produce sensitization or "pseudo-conditioning." To the extent that this type of change develops in such a control series the conclusion that true conditioning occurs with the same stimuli in a paired series must be discounted.

Sensitization in *Amoeba* is produced by repeated stimulation of the leading pseudopodia from a bright light as the organism advances. Locomotion is more readily stopped on later trials in a series [26]. An alternative way of increasing the effectiveness of light in producing this same behavioral result is by using a more intense stimulus. This fact seems to confirm the appropriateness of the term "sensitization" for the process in question. A physiological explanation for this modification must be sought in terms of some fairly long-lasting protoplasmic alteration.

A systematic series of studies of sensitization effects with other invertebrates would be desirable, but none exists and what evidence there is for this process comes from isolated studies with varying techniques. Experimenters have done more comparable studies at different levels in vertebrate forms. Goldfish, cats, monkeys, and human babies all prove susceptible to sensitization. The generalization of a sensitized response to a wide range of stimuli is observed in some of the experiments. Much work is still needed to determine what, if any, relation exists between such generalized sensitization and the species used. Harlow [16] has shown that goldfish can be "pseudo-conditioned" so that they respond more readily to audio-vibratory stimuli for at least three weeks. The sensitizing procedure involves stimulating them electrically to produce rapid fin and body movements for twenty or thirty trials. A similar technique used with cats or monkeys makes the animals highly reactive when a buzzer is sounded. The change in behavior is not specific to the experimental situation in the goldfish or cat, whereas for the monkey a discrimination of the environment enters into the sensitization and the animal tends to react only in the same or closely similar surroundings to those in which the sensitizing procedure occurred [14]. This fact introduces a significant variable correlated with species. For the monkey a true learning process accompanies the sensitization. Environmental stimuli participate in a significant way by virtue of a discriminative association. This difference between the fish and the primate is one of degree and one that becomes more or less prominent under various experimental conditions.

Stimulus Substitution

When occurrence of a response to a previously neutral stimulus depends upon the pairing of that stimulus with another that effectively elicits the response, we speak of stimulus substitution. Also called classical conditioning and respondent conditioning, this procedure is effective with flatworms and with at least some representative species through the highest vertebrates. The learned association between the CS (conditioned stimulus) and CR (conditioned response) sometimes involves an association between the CS and US (unconditioned stimulus). Figure 7-3 is a diagram of the two possible alternatives. Theorists have argued whether one or the other type of association is fundamental or whether there is any need to conceive of more than one of these mechanisms. To encompass all empirical data we need both concepts. Most studies of conditioning can be described, however, in terms of the S→R paradigm. We shall need to return to this question later in the chapter.

Classical Conditioning in Flatworms. The planarian *Dugesia dorotocephala* has been studied in a classical conditioning experiment with careful controls to rule out sensitization [52]. Light and shock were paired when the worm was moving in a straight line. A turn or a contraction was the worm's response to shock. The control group given repeated shocks unpaired with light showed no increase in number of responses to light. Other groups given 150 trials to light alone or 150 trials without stimulation showed no progressive changes either, with the possible exception of some reduction in the number of "spontaneous" turns. Significant increases in turns and in contractions in response to light as a function of the number of paired trials were shown by the experimental group.

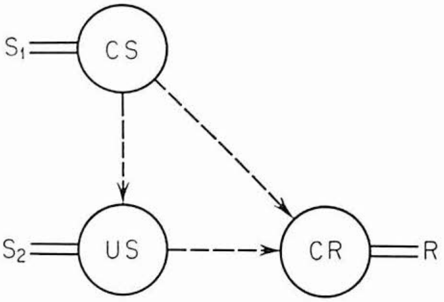

FIG. 7-3. Stimulus substitution. The stimulus S_1 is ineffective with respect to eliciting the response *R* prior to learning. S_2 is the adequate stimulus. Broken arrows indicate the associational routes whereby S_1 might become the sufficient stimulus. The direct CS → CR route has the advantage of theoretical simplicity. Where evidence points to a CS → US route, the problem becomes a neurophysiological one, but has behavioral implications. This implies, for example, that the response may be blocked temporarily during learning without disruption of the acquisition process. Some instances of stimulus substitution require this S → S explanation (see text, pp. 191–192).

The conditioned responses rarely turn out to be exact duplicates of the original responses to the US. This has been used as an argument against a concept of simple stimulus substitution in the learning of higher vertebrates, but it is also a problem of planaria. In the study just cited, response to the US was primarily a contraction of the worm, and the response to the CS was predominantly a turning to the side. The following explanation is suggested by the experimenters: "The turning response may have been a part of the unconditioned reaction, but was obscured by the more generalized contraction of the entire body" [52, p. 68]. Actually, the numbers of contractions taken by themselves do show an increase between the first 50 and the third 50 conditioning trials which is significant at the 0.01 level of confidence, as is the increase for turns. We conclude that even in flatworms conditioning involves a fairly complex response system and that the conditioned response may change in its characteristics during conditioning as a function of the relative contributions of components within the complex. We find another example of this in the study of learning in snails to be described next.

Conditioned Food-taking Responses in Snails. Students of psychology are well acquainted with Pavlov's technique for developing conditioned salivary reflexes in dogs. In addition to salivation Pavlov mentions other associated food-taking responses, such as anticipatory mouth movements and chewing. Some forty years ago an American contemporary of Pavlov, Elizabeth Thompson, applied a similar technique to a study of learning in the snail [50]. She asked the question: Could a pressure stimulus applied to the foot of the snail, which normally inhibits any ongoing mouth activity, serve instead as a conditioned stimulus for the mouth-movement response to food? Her stimulator enabled her to apply a small piece of fresh lettuce to the mouth at the same time that pressure was exerted a short distance behind the mouth to the animal's foot. She could also apply either stimulus alone.

Physa gyrina is a species of snail that normally suspends itself upside down from the surface film in quiet water. The foot and mouth are thus exposed and may readily be observed or stimulated. The experimenter habituated her snails so that they no longer dropped away from the surface when incidental mechanical disturbances were transmitted through the containing jar. Stimulation from the food, the US, was brief and was immediately followed by a series of mouth movements. The number of movements was a measure of the strength of response. Under 24-hour food deprivation the average was 5.86 mouth movements to one touch with lettuce, the opening and closing movements coming rhythmically at a rate of one cycle in 1.3 seconds.

When food and pressure to the foot were first combined, there was no response to food. In six snails, responses to the combined stimuli began after 60 to 110 trials and then averaged 3.42 mouth movements per response. The rhythm of these responses was consistently a little faster than the original response to food alone. Combined stimuli were presented for 250 trials. Thompson then found that pressure alone gave mouth responses. The rhythm of these CRs was the same as that for the food-with-pressure stimulation. Responses to foot pressure alone extinguished over varying numbers of trials, depending on the animal and the number of trials given per day. The effect of training persisted as long as 96 hours but was not tested for durability in the absence of daily extinction trials.

The conclusion is clear from these and many other studies of conditioned responses that, when accurate descriptions are obtained of the behavior to the US, the CS, and the two when paired, differences are found which reflect the functional properties of the particular stimuli employed by the experimenter. The concept of *stimulus substitution* is useful when we recognize that more primitive organisms as well as higher animals show such differences between the UR and the CR. These differences have sometimes been used to argue that the conditioning concept does not apply to higher mammals. More to the point would be the careful study of their nature and of the environmental and physiological parameters which bring them about.

Instrumental Learning

Instrumental learning is usually studied in situations which permit the animal freedom to initiate a variety of responses. The degree to which experimenters control the animal's responses varies widely from one study to another. The essential identifying feature of instrumental learning is that a learning "trial" is completed when and only when a particular response or sequence of responses by the animal results in a reinforcing (rewarding) consequence. The reinforcing consequence may be a simple event, such as the occurrence of a stimulus, or it may be a complex outcome, such as the finding and eating of food. Escape from harmful stimuli or from places where such stimuli have occurred previously are examples of reinforcing consequences. The animal is in each instance making responses which are instrumental in producing a specific kind of reinforcement by virtue of the experimental procedure used. Escape and avoidance conditioning, learning with primary reward, and learning with secondary rewards are descriptive categories which emphasize the operation of the *law of effect* in instrumental learning. These categories designate the more obvious aspects of the learning task without being mutually exclusive. We seldom know with certainty that a reward is exclusively primary or secondary, and there is usually some element of escape in a so-called "positive" reinforcement. This point becomes clear when a homeostatic mechanism can be identified.

Phylogenetic Comparisons in Instrumental Learning. We might expect to find that this somewhat more elaborate form of behavior modification would be restricted to the higher animals. Actually, instrumental learning is readily demonstrated in most representative animals from worms to man. A ganglionic nervous system with sufficient ganglionic massing to provide coordinating "centers" is one prerequisite, and this must be accompanied by an action system capable of bringing about a significant change in the environment—the reinforcement.

Only the simplest stimuli and responses are utilized in well-controlled or "pure" instrumental learning studies. This exemplifies the S→R learning paradigm free from contamination by intermixtures of perceptual learning or motor skills. Learning theorists [49, Chap. 2] would think first of pigeons pecking at small windows [10] or rats pressing a bar as good examples of instrumental learning. By concentrating motivational needs on the food or water that is sparsely provided by the animal's responses, most of its waking activity can be centered on the necessary response. Among the species most carefully studied thus far, experimenters find a remarkable uniformity in the temporal properties of this acquired S→R behavior [47]. As Skinner points out, the differences among species are in the anatomies of organisms to which the experimenter must adapt his procedure, not in the effects of reinforcement schedules on response rates.

Complex Eliciting "Stimuli." The precise nature of the stimulus which elicits the learned instrumental behavior is sometimes only loosely definable. We may point to the red or green circle of light shining before the pigeon or to the bar in the Skinner box for rats. The bird responds primarily to what it sees. Vision is less important and not really necessary to the bar pressing of the rat. When a somewhat more complicated case of trial-and-error learning is examined, the stimuli become even more difficult to specify. Much work has been done to determine the relevant cues in maze learning. This work shows that the cues are multiple and partially interchangeable, even in advanced stages of learning [25, Chap. 17].

Whether rats, earthworms, or human beings learn mazes, prior familiarity with similar mazes as well as opportunity to explore the specific maze to be learned contributes to the learning which is completed under reinforcement. Not all the learning required in this problem is instrumental learning. Simultaneous and successive patterning of stimuli integrate associatively the cues which come later to elicit the instrumental behavior sequence. This prior "cognitive" aspect of complex trial-and-error learning is closely related to the processes to be considered next.

The Learned Integration of Sensory Patterns

When an animal behaves in response to an isolated change in the environment, such as a flash of light or onset of a tone, the S→R concepts serve well to describe the experimental data. For experiments done in a complex supporting environment with important temporal and spatial relations between stimuli, S→R descriptions have failed to account for all of the data which some investigators have reported in a different descriptive language. An S→R language ignores complex relationships of stimuli (and also of responses) which a less elementaristic description is able to retain. The molar or wholistic description may fail, on the other hand, to specify environmental and behavioral details which are crucial. A word picture of the "starting box," the "route," the "goal," and any other significant "places" in the maze is too often incomplete. More than one study reported in this way has had to be reanalyzed and then repeated with important cues specified.

Fortunately the S→R and the molar languages are not incompatible. They overlap sufficiently to permit translation and mutual supplementation. We now know that stimuli are essential for the learning about "places" which is accomplished during movement of the animal through the maze. We know that the animal learns to make both specific responses and more general orientations. Acts of locomotion need not be linked together like an S→R chain. Whether specific turns or general directional responses will be learned we now know will depend on the availability of stimuli which are either highly specific to a given choice point or, as in the case of a distant light source, are consistently available throughout the maze for integration with a sequence of local stimuli.

In the recent "place" versus "response" learning controversy, learning theorists raised the question: Do animals learn "where" the food is in a maze, or do they learn a specific turning response at each choice point? Experimenters have by now repeatedly confirmed the finding that both processes are involved in spatial learning. The relative contributions of each process vary according to the stimuli that are available [12]. Apparently conflicting views of what is learned by the animal have thus turned out to be supplementary rather than mutually exclusive. But why were the S→R language and the S→R concept of association inadequate?

Experimental psychologists have neglected perceptual learning. There is no direct behavioral measure of it, if by direct we mean that we can record an immediate change in behavior. By definition, the sensory-sensory integration within and between sense modalities can occur in the absence of any overt response. To measure the effects of strictly sensory associations and the consequent change in an organism's discriminative and integrative capacities, experimenters usually find it necessary to work through a two-stage program. After an initial stage which involves exposure of the organism to the relevant sensory pattern(s), a second stage is introduced in which a behavioral indicator is developed, typically by arranging for some instrumental behavior to gain a new dependence upon the pattern which was perceptually integrated in the first stage. Latent-learning studies constitute one important set of examples of this approach. A "pure" case of this two-stage method is the experiment of Gibson and Walk described in the next section.

Learned Integrations of Visual Forms. The visual environment of birds and mammals is, generally speaking, very complex. Physical-energy distributions of a visual stimulus can be sufficiently simple to be amenable to numerical specification or they may be so complex that no practical quantitative designation can substitute for a picture or diagram. Somehow organisms do integrate the complex distributions into units. Gestalt psychology has pointed out that certain configurations are unified easily. To what degree "natural" configurations are innately assured, and how much early learning contributes, the animal psychologist is beginning to discover.

When a single restricted area of the visual field is sharply differentiated from the remaining portion, animals orient toward it whether or not they have had previous visual experience. Birds learn quite rapidly to respond differentially to color and size characteristics of such figures, often modifying innate preferences in the learning process. Neither pigeons [46] nor young bantam chickens [55] learn to discriminate visual forms rapidly if they have not had previous experience with a patterned visual environment. Studies of the effects of early perceptual experience on later learning in rats [11], chimpanzees [41], and man [8] support Hebb's [20] theory of the development of neural phase sequences in sensory projection systems. The essential feature of the theory is that sensory contiguities generate neural cell assemblies and sequences so that stimuli gain a more consistent control over central neural structures as they recur in predictable (as opposed to random) patterns.

An outstanding example of how a specific form discrimination in adult rats may depend upon visual-form stimulation during growth supports the conclusion that intrasensory (stimulus-stimulus) integration is in part a function of associative learning. Gibson and Walk [13] raised a control group and an experimental group of albino rats under identical conditions except that two equilateral triangles and two circles were fastened to the sides of the cages of the experimental animals. White walls surrounded each cage. The forms were solid black metal.

At ninety days of age both groups of animals were started on discrimination training. They learned to push open small doors in the center of either one of a pair of black forms that were the same shape and slightly smaller than the forms used in the living cages of the experimental group of animals. Half of the animals in each group were rewarded with food for going to the circle and others for going to the triangle. Figure 7-4 shows the difference between the experimental and control groups in learning to discriminate these geometric forms.

The control group of rats in this experiment had not been completely deprived of form stimulation. They could see their cage mates, the wire mesh of their cages, which was in the form of ½-inch squares, a water bottle, and food. Dark rearing or rearing with only diffuse light have even more pronounced retarding effects on the abilities of animals to utilize visual stimulus patterns. Birds, rabbits, cats, dogs, monkeys, and chimpanzees so reared are at first unable to avoid obstacles, and they learn gradually to orient toward and respond discriminatively to objects. The period of incapacity is longer in the primates than in the other vertebrates.

Evidence for Cortical Participation in Sensory-sensory Patterning. Brightness and pitch discriminations are learned by mammals even without visual or auditory cortex. When visual forms or auditory patterns are to be discriminated, the corresponding sensory cortex becomes essential. Learned discriminations of auditory patterns (simple three-tone sequences) are lost after complete ablation of the auditory cortex of monkeys or cats [7, 32]. Nor can they be relearned after ablation. The component tone frequencies taken singly can still be discriminated. These recent experiments show that the essential contribution of the sensory cortex is in relating one tone to another in a discriminated pattern. The problem for the animal is that of making one response to a simple melody and then changing the response when the melody changes. This is a discrimination which requires an S→S integration.

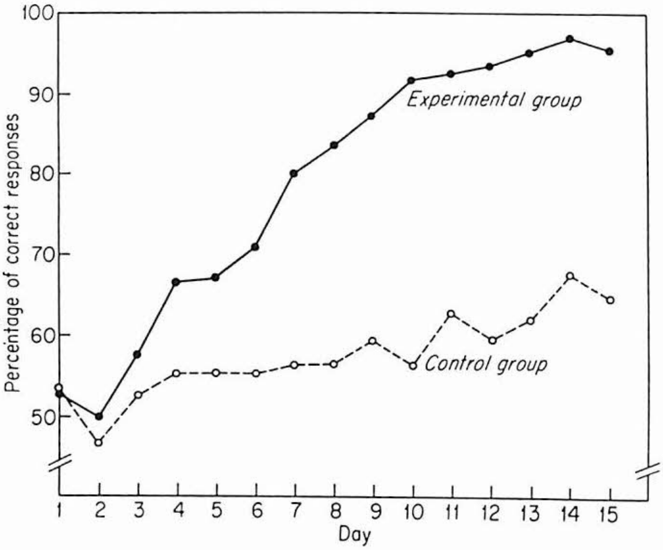

FIG. 7-4. The learning curves for two groups of rats. The experimental group had been exposed to triangles and circles in their cages regularly in early life; the control group had lived in wire-mesh cages surrounded by white walls and white ceiling. [*From Eleanor J. Gibson and Richard D. Walk, The effect of prolonged exposure to visually presented patterns on learning to discriminate them. J. Comp. Physiol. Psychol.,* 1956, **49,** 239–242.]

Physiological evidence for sensory-sensory learning is also provided by a study of escape and avoidance conditioning in which the one essential cortical area found was that in which the unconditioned stimulus was represented. Removal of the cortical representation of the US destroyed the learned behavior in both a classical escape conditioned response and in instrumental learning of the avoidance type [58]. These experiments show that what looks like S→R learning must sometimes be S→S→R learning (Fig. 7-3). The fact that the S→S part of this paradigm is critical argues incontrovertibly against the view that all learning is a change in sensorimotor "connections."

Conditional Discriminations as a Measure of Species Differences. The *conditional discrimination* procedure of Lashley [24] requires that animals learn to respond differentially to varying combinations of two or more aspects of stimulus objects or "cues," each aspect being ambivalent except in the presence of the other(s). To illustrate, if we present the animal with two circles that differ in size, he learns to take the larger one, if two triangles, the smaller. As a next step we can mix in trials with a triangle and a circle shown together. Which the animal must take to get the reward depends on whether they are *both* large or both small. This technique provides for independent variation in the specific stimulus components of an S→S pattern. The complexity of a problem can vary with the number of aspects to which the animal must respond simultaneously. Nissen [34] has employed this technique for testing the limits of chimpanzee conditional-discrimination behavior. His subject was able to combine five independent aspects of visually discriminated stimulus objects. This required a long training program. Even an adult human being would have difficulty with this problem until he wrote down the solution in a formula: "if a, and if b, . . . then x." Monkeys have achieved some multiple-sign discriminations with three and four ambivalent components. Subprimates have not been tested systematically with more than two components, on which some species succeed readily as long as "appropriate" components are utilized in designing the problem. Harlow [18] reviews many studies of this kind, particularly the work on primates, and shows that difficulty may hinge as much on the choice of component aspects as it does on their number. Standardization of methods has not proceeded far enough to permit more than the tentative conclusion that higher primates are capable of learning more complicated ambivalent-cue problems than are subprimates.

The kind of flexibility of response required in conditional reactions appears in a rudimentary form even below the vertebrate level. For an experiment on *Octopus*, Boycott and Young [4] trained their animals to inhibit their normal approach to a crab if a red square was immediately in back of the crab and to approach and seize the crab on a white square. (For some animals, presence of the white square was the condition for avoidance.) This is perhaps the lowest order of conditional behavior involving learning, for here the basic approach response to the ambivalent cue, the crab, is apparently innate or learned early and the second stimulus, in this case the background cue, is not ambivalent.[*] The experimenters go on to show that removal of the lobus frontalis superior abolishes the discrimination and the ability to relearn it. The operated animals either attack both stimulus combinations or neither.

There is no experimental demonstration in lower phyla of a similar learned contribution to the discrimination of combined simultaneous and independent aspects of a stimulus pattern. It is the increasing complexity of what might be called *contextual learning* that distinguishes the environmental control of behavior in higher organisms. On the response side there is in general a corresponding increase in refinements of the capacity to learn to manipulate the environment, but this comes later in the evolutionary scale. Refinement of discrimination precedes refinement of response skills.

One-trial Learning and Delayed Response

Some organisms utilize single exposures to stimuli or to a stimulus-response consequence as the basis for later discriminative behavior. In a few species there are specific stimuli to which one-trial learning occurs on an innate basis. Insects or birds most often reveal unique susceptibilities to particular classes of chemical, visual, or auditory stimuli which ensure rapid learning. While relatively few examples of this have been demonstrated experimentally, work on imprinting and other forms of one-trial learning is sure to bring new evidence.

Learning of Places. In a broad sense, rapid learning of place discriminations improves with phylogenetic level. An opportunity to "learn to learn" is always a necessary antecedent to rapid place learning. Insects show it only in familiar territory. One of the best examples of this ability is found in the digger wasp, *Ammophila campestris* [1]. The mother wasp of this species usually tends two, and occasionally three, nests daily over a period of several days. Each nest contains an egg or larva. The wasp supplies additional food in the form of caterpillars which she has killed or paralyzed. Her behavior during the day is influenced very specifically by the supply of food she finds in a nest on her first visit of the day. By removing or adding caterpillars to the nests, Baerends was able to study this one-trial learning in detail. He found that the amount of food present on the mother wasp's first visit was the cue that determined which nest she supplied by return visits and that the return visits could be delayed for quite a number of hours. This level of performance when measured by the length of delay possible is comparable to that of many higher mammals tested under the most appropriate laboratory conditions. There is no evidence, however, that the one-trial learning can be obtained when any cue is substituted for quantity-of-caterpillars-in-nest.

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[*] The reader should consult Nissen's [33, p. 27] distinction between ambivalent cues whose significance is dependent upon context and ambivalent, nondifferential stimuli, such as the crab lure in this experiment.

Primates and other mammals begin life with no ability to use place cues for one-trial learning. After restriction of early experience to only the simplest kinds of place orienting, rats, cats, dogs, and primates are demonstrably poor in new place learning [11; 41; 43; 53, p. 130]. They may be quite unable to do spatial delayed responses. With experience in a well-differentiated spatial environment, individual animals of many mammalian species develop abilities for delayed response and rapid positional-discrimination reversals. A large variety of designating cues becomes effective for eliciting these kinds of behavior.

Spatial learning by earthworms in a T maze gives a procedural model which has been used to compare species. The results of these comparisons demonstrate some significant differences among vertebrates of different classes and between vertebrates and invertebrates. Sheer-error scores show that positional discriminations in the T maze are more efficiently learned by the higher vertebrates. We saw earlier that one-trial reversals of such a positional response are possible in rats but not in the sow bug. The terrapin achieves one-trial reversals somewhat less readily than the rat but considerably more efficiently than the newt [45]. The experimenter who compared terrapins and newts using identical apparatus and procedures concludes that terrapins show greater plasticity of behavior because of the more efficient organization of sensory impulses by the reptilian nervous system with its neopallium.

Rapid Identification of Objects. The first learned recognition of objects by higher mammals, whether diffuse-light-reared or dark-reared, requires many learning trials. Later a great variety of objects can be identified on the basis of an isolated experience. Instrumental behavior can be elicited effectively by such a stimulus object after one differential reinforcement. The higher primates clearly show the maximum final level of efficiency in this process, at least for visually apprehended objects. In man, auditory cues come to share this effectiveness. Such perceptual capacities give us the outstanding measures of psychological advancement in evolution. The visual recognition of one individual animal by another can be included in this category. Systematic investigation of this "social" identifying capacity has not gone far on a comparative basis, but we know that species and even individuals within species differ in the degree to which they develop sensitivity for discriminating each other as individuals.

The comparative study of object-discrimination learning sets is a recent development in the study of "learning to learn," which began with Harlow's work on rhesus monkeys [17]. The method has been used with children, chimpanzees, several species of monkey, and cats. The results of these comparisons give us clear differences between species in the rate at which the animals learn to learn and in the level of accuracy shown on the second trial of each new problem. Cats are inferior to primates, and marmosets are inferior to rhesus monkeys [27, 56]. Figure 7-5 shows how much more efficiently rhesus monkeys learn during an extended series of 6-trial problems when compared with marmosets. Chimpanzees reach trial-2 accuracy levels of 95 per cent [19], while cats reach an average of 75 per cent accuracy on trials 2 to 10, the trial-2 level being scarcely above chance [56]. Difference in sensory capacity cannot be excluded entirely as a contributing factor, but such a variable

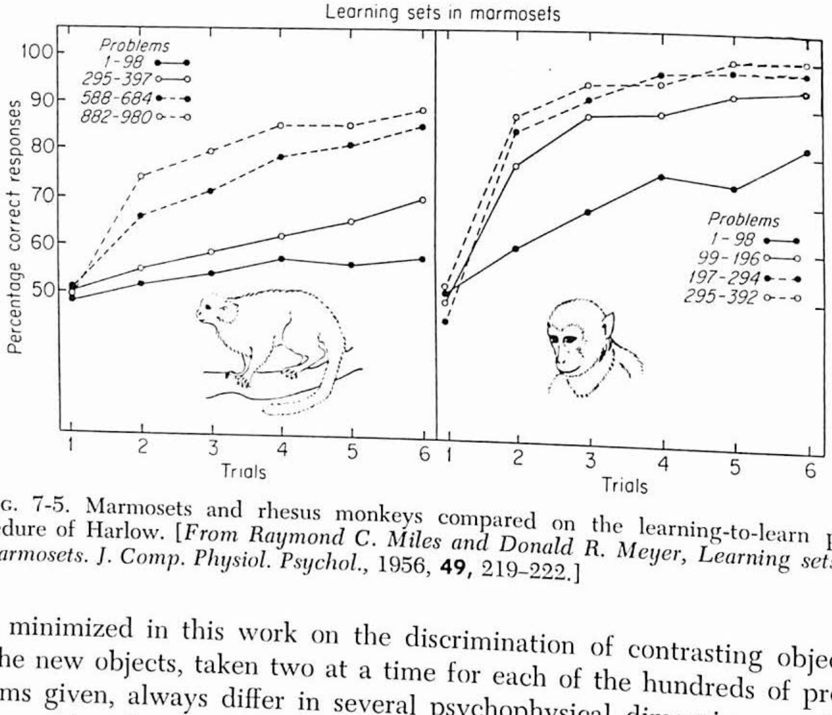

FIG. 7-5. Marmosets and rhesus monkeys compared on the learning-to-learn procedure of Harlow. [From *Raymond C. Miles and Donald R. Meyer, Learning sets in marmosets. J. Comp. Physiol. Psychol.*, 1956, **49**, 219–222.]

is minimized in this work on the discrimination of contrasting objects. The new objects, taken two at a time for each of the hundreds of problems given, always differ in several psychophysical dimensions: outline form, size, brightness, and color. Poorer performance in the cat is correlated not with random response but with a tendency to continue responding to the object chosen on initial trials.

Speed of Learning as a Correlate of Phyletic Level. The mere presence or absence of one-trial learning is only grossly correlated with psychological complexity. This capacity is absent in lower invertebrates but clearly occurs in some arthropods. In fish, birds, and mammals, delayed response based on positional cues has been demonstrated, and the ability parallels closely that for "detour" behavior or a primitive kind of "insight."

A more discriminating measure of phylogenetic advancement is that which requires object recognition on the basis of one experience. As we have seen above, this kind of learning is sensitive enough to differentiate between lower and higher vertebrates, between lower and higher primates, and even among individuals of a given species with differing environmental histories. Special training and a varied or highly structured visual environment improve the capacity of an individual animal for pattern or object recognition and for spatial learning. The capacity to discriminate and to show memory for a place, object, or sound pattern, for example, appears to depend on cumulative learning. This capacity must be distinguished from mere capacity to respond to change [20, pp. 26 to 32]. The degree to which it can be developed reaches a maximum in higher primates.

Object-discrimination learning sets represent a learning-to-learn or interproblem transfer process. They seem to require a high degree of configurational learning in which a unified "cue" attains its unity and recognizability through sensory-sensory associative experiences. In higher organisms these cues are unique in their prepotency for acquiring sign properties in behavior.

Learned Integration of Complex Responses

The separation of innate from learned aspects of response coordinations is difficult, yet there is no question that a learning process enters into the more refined motor behavior of higher organisms. For learning which includes a response component, sensorimotor learning is the simplest and the phylogenetically primitive form. Much of what has been said in this chapter about conditioning and instrumental learning applies to this S→R aspect of response modification. But this paradigm is insufficient, and an R→R coordinating component will have to be considered if the motor side of learned behavior is to be fully understood.

Lashley pointed out many years ago that behavior cannot be analyzed into mere stimulus-response chains because on the response side such a sequence would have to be much slowed down to permit feedback between each of the varying response units [23]. The pianist, he pointed out, develops larger response integrations from the note by note performance of the novice to the arpeggio units of the expert wherein cortical reaction time is too slow to permit afferent and efferent conduction between each note. Furthermore, since S→R learning requires separation of S from R by 0.25 to 0.50 second for optimal conditioning, fast-moving skills would be acquired with poor efficiency if the S→R chaining mechanism were the only one available. As Lashley's study showed, the elimination of sensory return from the responding organ does not preclude accurate gradations of strength and direction of movement so long as the subject has a feel for the starting position of the digit or limb.

Manipulative and acrobatic skills require response sequences that are accurately graded and timed in advance, with component movements related precisely to each other. Without denying the imperativeness of sensory confirmation (reinforcements) during acquisition, we must concede that skills gradually attain the property of autonomous motor systems. Increasingly complex units of these skills become self-containing or automatic, having their own configurational properties. Response-response integration based on a contiguity learning principle is demanded by the properties of motor behavior. Of necessity, the analogy between this process and that of learned perceptual integrations implicates *phase sequences* in the motor areas to correspond with those invoked for sensory areas of the central nervous system [20].

Animals with Exceptional Capacity for Motor Adaptations. Circus and zoo biologists and experts on marine mammals can tell us more about the skills which animals learn than the comparative psychologist can. We are likely to think of apes and monkeys as performing the most complex, learned postural and manipulative acts. They are neurally, skeletally, and muscularly well equipped for such behavior. Lower vertebrates and invertebrates are not. The motor skills of many mammals, when learning opportunities are maximized, are impressive. The balancing acts of seals and the basketball shooting of porpoises are firm evidence for an extremely fine motor control in sea mammals. The elephant shows remarkable motor coordinations and learned-response skills. The neuromuscular basis for this behavior is not as well understood as that for primates, which in itself has been given little attention since the work of Lashley and of Sherrington. The problem of response coordination constitutes a challenging area for the neuropsychologist and comparative anatomist.

Systematic study of developing postural and locomotor skills indicates that in higher primates, at least, there is a final refinement of coordination that depends upon practice but that this practice is largely self-initiated [42, p. 170 ff.]. Whatever motivation is necessary seems to reside in the activity-for-its-own-sake. There is little doubt that maturational processes contribute the foundation stones and that the development of basic motor skills for bodily activity is so much a part of biological growth that those refinements which constitute the learned aspects of it are not easily disentangled.

The experimental study of R→R learning would be advanced greatly and would serve both practical and theoretical ends in comparative psychology if response-deprivation studies comparable to some of the work on sensory deprivation could be carried out. Response skills, like perception, show the cumulative advantages, and interference effects, of prior learning on new learning. An initial investigation of this kind has been done with a chimpanzee by Nissen and associates [35]. Manipulative skills of the hands lagged behind those of the mouth in this animal, whose hands and forearms were loosely encased in mailing tubes for the first thirty-one months of life (Fig. 7-6). The use of forearms in locomotion and in sitting postures was affected. Taken in comparison with Carmichael's classical study of the anesthetized amphibian [6], in which locomotion was unimpaired, this result points to phyletic differences that need much further study.

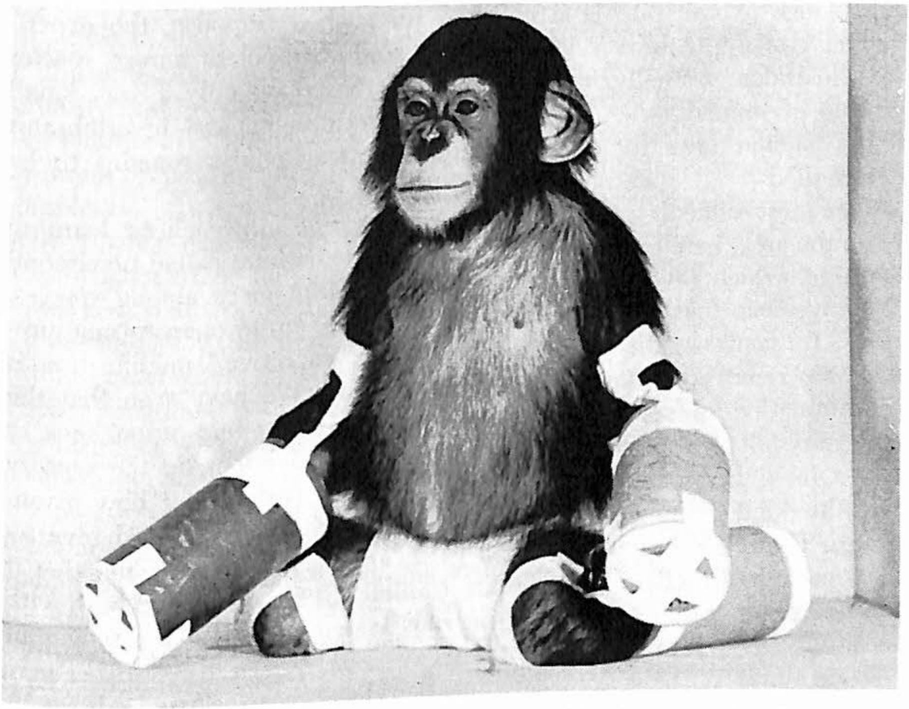

FIG. 7-6. Chimpanzee, Rob, was deprived of the use of his hands and feet for manipulation and certain kinds of tactual-kinesthetic experience from birth to two and one-half years. Manual skills, postural behavior, and tactual localization were all affected. [*From H. W. Nissen, K. L. Chow, and J. Semmes, Effects of restricted opportunity for tactual, kinesthetic, and manipulative experience on the behavior of a chimpanzee. Amer. J. Psychol.*, 1951, **64**, 485–507.]

UNSOLVED PROBLEMS AND THE SEARCH FOR PRINCIPLES

The laws governing changes in the frequency with which a given stimulus will elicit a given response [10, 49] are, as we have already seen, applicable to many species. More work is needed to determine just what differences there may be among species. Skinner [47] argues for the generality of the principles across species. Rate of responding varies more, according to the data obtained on vertebrates (birds and mammals), with the nature of the response than with the species. The species is important only in so far as the particular animal's structure determines the appropriateness of the response or manipulation which it must execute. Once a base rate is established for such a response, the experimenter can apply laws relative to this and extrapolate across species with abandon. Actually, this conclusion is based on only a very small sample of animal types. Whether lower vertebrates and invertebrates follow similar laws for partial reinforcement schedules remains to be determined.

The most difficult problems in a *comparative* approach to learning lie in the area, here called S→S learning and sometimes called perceptual learning, which reveals the most significant differences among species. We have seen that sensorimotor associations are quite open to measurement. By contrast, the stimulus-stimulus, or "cognitive," modification is one step removed from behavioral observation. We have seen that the discrimination of sensory patterns is highly dependent upon sensory neurophysiological structures and specifically dependent on the sensory *cortex* in higher mammals. We know relatively little about how extensive this kind of modification can be in lower vertebrates and invertebrates. There is no question that it exists among lower forms and that it is far more limited than in mammals. Limitations are correlated both with the degree of elaboration of the nervous system and with the ranges of sensitivity built into the sense organs.

Four types of behavioral modification have been classed above as arising primarily from some regular exposure to stimulation. These we called habituation, sensitization, stimulus substitution, and sensory-sensory integration. The last category can be subdivided into associations within a sensory modality, such as audition or vision, and associations between modalities. Both kinds are normally dependent upon recurrent events (or regularities) in the environment. The result, in general terms, is either increasing regularity of behavior or a shift from one kind of regularity to another.

Some of these regularities change in accordance with a classical conditioning paradigm, control of a particular response shifting from one stimulus to another or at least occurring more frequently to one stimulus after "reinforcement." Other changes in the regularity of behavior can only be explained in terms of S→S structurings. Environmental events which have not previously occurred together may initially produce no consistent response or a highly variable one. After frequent co-occurrences, this combination of sensory events begins to call forth a response which it has not previously aroused. A little later, moderate deviations from this pattern will suddenly arouse fear and avoidance. Such avoidance need not have occurred previously in the life history of the animal.

The successive stages in the behavioral effects of stimuli which repeatedly occur together as a pattern may be described as follows: (1) a period during which there is little or no response—a kind of form blindness in the case of vision and nonrecognition of melodic sequence in the auditory sense mode, (2) a period of gradually increasing familiarity with obvious visual orientation or attentive listening, (3) a sudden emotional disturbance when the pattern deviates from the familiar by some optimal amount. This fear of novel stimuli depends upon the completion of stage 2, which is the sensory-sensory associative process. With further exposure to the deviant pattern the fear and avoidance subside, just as in the simpler examples of habituation. Instead, there may develop an approach response (stage 4) in which active exploration by the animal is the dominant and persistent behavior. None of these alterations of *response* are learned. They are unconditioned, or innate. Their appearance is the overt and observable evidence that the sensory organization, which is the learned component of the new behavior, has reached a given stage of development.

Further study of this sequence of responses to repeated patterns of stimulation in representative animals is needed. In birds [55] and some mammals it is clear that *imprinting* experience has the property of moving the animal through stages 2 and 3. An experiment by Welker [57] with young chimpanzees was aimed at an investigation of stages 3 and 4. Welker followed these stages as a function of the age of his animals. He also plotted the gradual change in response to specific three-dimensional patterns (objects) as a function of the cumulative time of exposure to each of them (Fig. 7-7). The cycle from timid regard with avoidance to immediate approach and manipulation was repeated with each new complex stimulus. Welker placed objects such as colored blocks, short sticks, or a coffee can in the young animal's cage. Daily tests continued until the chimpanzee spent fifty or more of a possible sixty 5-second periods touching the object in some way. Here is an example of a behavioral sequence that reflects perceptual learning and to which innate motivational mechanisms are closely linked. Enough experiments have been done to show that the sequence of changes in response appears in several selected vertebrates [20, pp. 241 to 245; 41, pp. 433 to 439; 43].

We may ask whether there is a common principle underlying all the S→S, S→R, and R→R types of learning which we have examined and whether these apply in all organisms. It is fair to state that learning theorists who have emphasized a given principle have always left out some kinds of learning. The most commonly accepted principle is the *law of contiguity*, which, if we allow some latitude within the problem of *what* must be contiguous, applies to all except the habituation and the sensitization types of behavior modification. The contents of this chapter carry the implication that a contiguity principle operates between stimuli, between responses, and between a stimulus and a response. The neurophysiologist must some day tell us why this is possible. Judging from the generality of the principles, we may expect that he will also tell us why this occurs in all kinds of animals, except those members of the four lowest phyla.

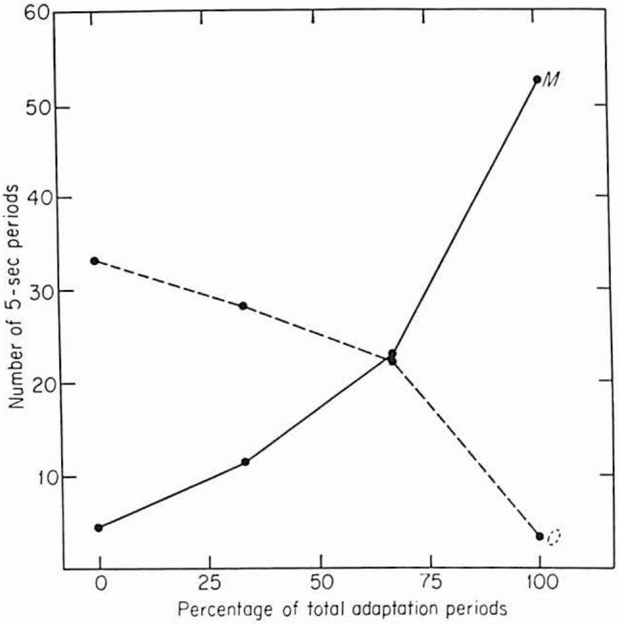

FIG. 7-7. Averaged response curves for five young chimpanzees, aged ten months to three years, when exposed repeatedly to new objects. At first the animals responded with timidity or fear. The dashed-line curve shows a gradual decrease of fearful watching (O = orienting) from a distance. The solid line shows the increasing amount of time that the animals gave to touching and playing with the objects (M = manipulation) as they could see them daily for a 5-minute period. [*From W. I. Welker, Effects of age and experience on play and exploration of young chimpanzees. J. Comp. Physiol. Psychol.*, 1956, **49,** 223–226.]

Does the principle of reinforcement, emphasized above in connection with instrumental learning, have a similar generality of application? The answer to this question is not known. Its possible operation in S→S and R→R learning is suggested in some examples, but a clear demonstration that reinforcement (in the sense of some critical event in the organism's motivational structure) must accompany the sensory or motor processes is lacking. There is some reason to accept this principle for the response aspects of learning and hence for both S→R and R→R integrations. Furthermore, there is a mass of compelling evidence that the neural representations of the motivational event are themselves associatively integrated into the S→R and the R→R processes. This crucial problem and the related concept of secondary motivation are treated in other chapters of this book (see specifically Chap. 6).

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CHAPTER 8

Complex Processes

Earlier chapters in this book have discussed the sensory and learning capacities of various organisms. In the present chapter we shall consider those processes which, although depending a great deal upon such basic capacities, emphasize the utilization of information thus gained. These are usually referred to as higher mental processes or cognitive functions. Whether they can be reduced theoretically to more elementary processes is a matter on which little agreement has been reached. In the absence of a universally acceptable theory, we shall concern ourselves with a description of several examples of the procedures and experimental results in this area.* In this way we can see similarities and differences among problems, procedures, and results in experiments on animals of different phyletic levels.

As we all know, in the middle of the nineteenth century, Darwin and Wallace propounded theories of organic evolution based on natural selection. These theories created a storm of controversy regarding the origin of man's bodily form. The storm probably would have subsided relatively quickly had the theory been restricted to structural form. However, Darwin's faith in the processes of natural selection led him to propose a continuity in mentality, emotion, and morality through lower animals to man. It was this proposal which raised the storm to holocaust proportions. To the scientific controversies were added moral and theological ones.

It became evident that a resolution of this (even now) unresolved controversy lay a long way from the armchair and fireside, comfortable though these might be. The task was to show that lower animals did, in fact, possess emotion and reasoning. At first the anecdotal method was accepted as the principal source of evidence for the presence of these processes in the animal. From natural-history sources, animal trainers, and enthusiastic observers came anecdotes describing reasoning, cunning, imitation, fear, anger, shame, and curiosity in animals. Because of the uncritical enthusiasm of many writers, the absence of knowledge of the historical antecedents of such behavior, and the obvious lack of controls, this method was gradually superseded by methods of experimental observation.

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In addition to the establishment of a gradation of performance among the various species, the investigator has the important task of determining why an animal responds the way he does when confronted with a given kind of problem. We need particularly to know how to present a problem to the animal. Adequate tests of any species's ability to solve problems of various types can take place only if the experimenter does not obscure the critical relations for the animal by inadequately displaying the problems to him. By what rules shall experiments be designed and presented so that they will measure those aspects of performance which reveal cognitive processes? For example, we may postulate that the perceptual process of infrahuman animals are similar to those of humans and that the human investigator need only consider what "looks right." But in so doing we may make the mistake implied in Bertrand Russell's statement, "The method of postulating what we want has many advantages; they are the same as the advantages of theft over honest toil."

Instead of depending on their own perceptual processes as a guide in animal experimentation, recent investigators have made intensive studies of the factors that contribute to the ease with which problems are solved by the infrahuman animal. From these studies have come results which delineate the perceptual organization of lower animals and which should serve as the basis for the rules of experimentation. What is more important, these studies have given us cause to reinterpret the results of older investigations. Many tasks once thought to involve higher mental processes because they were so difficult are now thought, instead, to have been difficult because the problems were presented inefficiently.

This chapter will place great emphasis on the kinds of experimental methods and arrangements which affect performance in tests of cognitive processes. We do this not because we hope to reduce all previously considered complex processes to simpler ones but because, by considering the various classical methods of testing complex behavior and the factors which affect it, we can achieve some notion of what it is that gives each test its uniqueness and what each test has in common with other tests. From data to be considered in this chapter it will become very clear that there is an impressive continuity of the so-called "higher" with the lower processes.

DISCRIMINATION LEARNING

By discrimination learning we mean the formation of a differential (selective) response to temporally proximate stimulus differences presented through the sensory channels: auditory, visual, tactual, etc. Notice that there are two aspects of this definition: (*a*) the detection of the difference and (*b*) the development of a consistent response relative to the differing stimuli. Variables affecting the former concern intensity levels, wavelengths, sensory modalities involved, spatial and temporal contiguities of the relevant stimuli, etc.; some of the variables discussed earlier in Chapter 7 on learning and later in Chapter 12 on the physiological basis of behavior are relevant to the latter. The fact that we are at present unable to measure independently the contributions of these two classes of variables to performance on a single problem has forced the experimental psychologist to investigate the problem by manipulating the variables of one type while deliberately holding the others constant.

Methods of Investigating Visual Discrimination Learning

Several methods have been used for testing visual discrimination. The most common one is the *simultaneous discrimination method.* In this method the animal is presented with two or more stimuli, response to one of which is rewarded. Its most important characteristic is that the animal is able to compare the stimuli many times before a choice is made. Other procedures have been developed which do not permit this comparing behavior. They are classed as *successive discrimination methods.*

In one such variation, sometimes called the *differentiation method* [2] or the *yes-no* method, only one stimulus, positive or negative (i.e., rewarded or unrewarded), is presented on a single trial. In this method the animal is trained to respond rapidly to the rewarded stimulus object and to inhibit response (for, say, 10 seconds) when the negative stimulus is presented. Another variation has been called the *sign-differentiated position response.* Typically, two or more identical stimuli are presented on each trial. When all are of one type, the reward is found at the left position; when all are of the other type, reward is found at the right position. Sometimes only one stimulus, *A* or *B*, is used to indicate whether the reward is on the left or the right.

Two different reward procedures have been used. In the *correction method* the animal, after responding to the negative stimulus, either reruns the trial until he is rewarded or he responds to the remaining objects in turn until he obtains reward. In the *noncorrection method* the animal is permitted only a single choice on each trial. The most important difference between the correction and the noncorrection methods is in the bookkeeping; it is impossible to translate one scoring system into the other. With the correction method, twenty-five trials may mean twenty-five, fifty, or more responses. On the other hand, with the noncorrection method, twenty-five trials means only twenty-five responses.

A variety of apparatuses have been used, most of which have been employed with slight modication for both simultaneous and successive discrimination. We shall describe their use for simultaneous discrimination only; the reader will have little difficulty envisaging their use in successive discrimination.

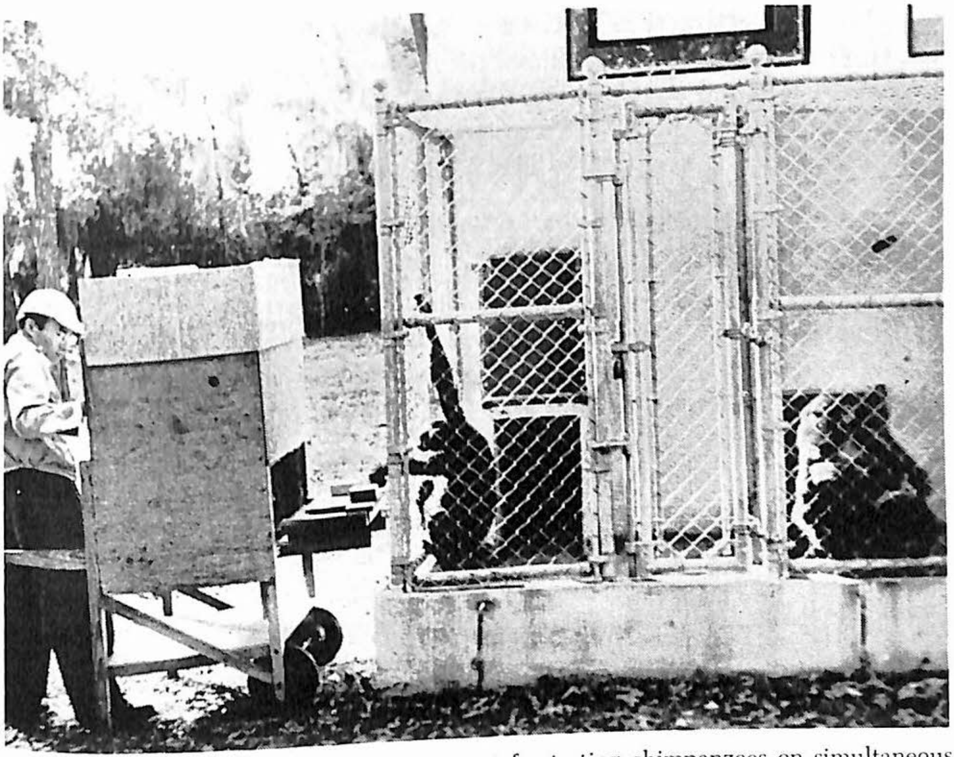

Fig. 8-1. Apparatus and general arrangement for testing chimpanzees on simultaneous discriminations at Yerkes Laboratories.

For small animals, such as a rat, a Y maze or a T maze is frequently used. At the yoke of the Y is presented the pair of stimuli, usually cards mounted freely. The rat executes his choice by nudging the chosen card out of his way with his nose. Because the rat must continue to run to the end of the alley, reward may be delayed for several seconds even though it selects the correct card. To avoid this, Lashley, a pioneer in this field, developed the jumping stand [32]. This device contains a platform and two adjacent windows several inches from the platform. The rat is trained to jump directly from the platform to one of the windows for food. Eventually the rat is trained to jump to the stimulus cards. Fields [10] increased the number of stimuli present at one time and placed four of these modified jumping stands in tandem. He obtained very efficient learning in the rat.

For animals with good manual dexterity, a pull-in technique developed by Klüver can be used. The stimuli are fixed to little boxes or cards attached to strings that can be pulled in by the animal. In another method the stimuli may be presented on a tray containing food wells under the stimuli. In this case the animal displaces a stimulus for its food well. Figures 8-1 and 8-12 illustrate the method. A procedure suitable for large animals is to place the reward in a box with a hinged lid. The animal must learn to open the box having on its lid the correct pattern.

Comparisons among Species in Visual-discrimination Learning

A few studies throw some light upon the capacities of different animal species in visual discrimination. Gardner trained horses, cows, sheep, and human aments (mental defectives–idiots and imbeciles) to obtain food from one of three boxes. The correct box was covered by a black cloth. In a subsequent study she and Nissen [11] tested ten chimpanzees and then summarized the entire set of data, all gathered under conditions as comparable as possible. In terms of making the correct response, the domestic animals had the best scores, followed next by aments and finally by the chimpanzees. Data for dogs [27], raccoons [62], and cats, all carnivores, indicate performance equivalent to that of animals of the Gardner study. Although data exist which lead one to suspect that birds might learn similar problems more slowly [67], a more recent study [63] has shown that, under appropriate testing conditions, doves can learn simple discriminations at speeds comparable to those for mammals. The rate of formation of a simple discrimination habit does not increase regularly from the so-called "lower" to higher phyletic levels.

Factors in the Stimulus Presentation Affecting Discrimination

Animals undergoing testing for discrimination do not respond unbiasedly to all aspects or dimensions of the stimulus situation. On the contrary, they selectively respond to certain ones, such as color, form, etc. If a particular bias is unsuccessful (the reward not being obtained), the animal shifts to another bias. This selectivity for one rather than another stimulus aspect is thought by many to represent one of the important component skills in a selecting process more complicated than simple associative learning. As is developed below, much of the information we have about this selective process has been obtained from analyses of the aspects in the stimulus display which affect discriminability. Those factors which are important in discrimination learning are also meaningful dimensions for comparing different species.

Color, Size, and Form. In any visual-discrimination problem the stimuli presented may differ in color (including differences in hue, brightness, and saturation) as well as in size, form, or any combination of these dimensions. Here is an important question: Does the animal learn to respond to most or all such possible differences between the rewarded and nonrewarded stimuli, or does he isolate a single difference and respond according to that difference? For example, if both color and size of the stimulus pattern *could* be cues to the reward, which would the animal use, or would he employ both?

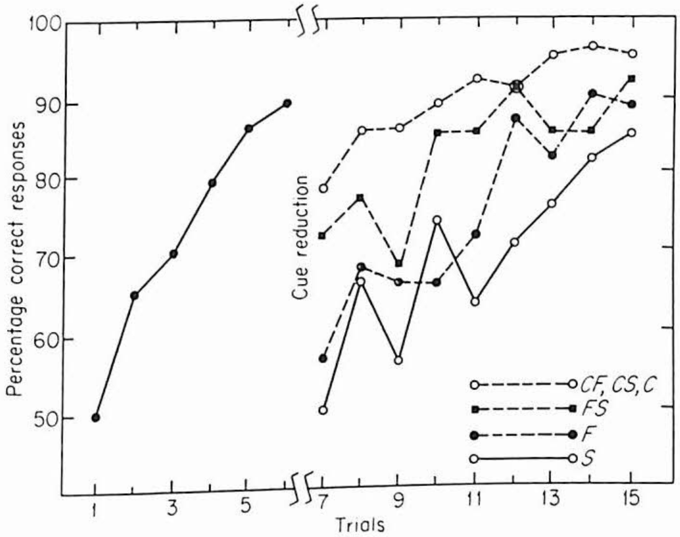

FIG. 8-2. The effects of cue reduction on discrimination learning. Monkeys were given six trials on stimulus objects differing in color (*C*), form (*F*), and size (*S*). On subsequent trials the stimuli differed in fewer ways, for example in color and form only.

Lashley [33] trained rats to discriminate stimuli differing in multiple dimensions and found, in subsequent critical tests designed to determine the basis of the discriminative response, that the animals had been responding to differences in a *single* dominant dimension. To see if these findings held for monkeys, Warren [72] trained four rhesus monkeys on ninety-six problems. During the first six trials of each problem, the stimuli differed in three aspects: color, form, and size. On trials 7 to 15, new stimuli were introduced differing in only one or two of these aspects. The results are shown in Figure 8-2. The curve on the left shows performance when the stimuli differed in color, size, and form, whereas data for the trials when one or two of the possible cues were eliminated are on the right. The top curve on the right denotes performance on the tests for discrimination when the stimuli presented differed in color and form, color and size, or only color. (All results from these tests were combined into one curve because the separate curves were practically superimposable.) When the test problems involved stimuli that varied only in size, performance was poorest. Color, in this investigation, was the most "helpful" cue. Warren [71] likewise found that discriminability of monkeys was an increasing function of the *colored* portions of "patterned" stimuli (see below). This trend has appeared in data gathered with chimpanzees, although the effect was not so pronounced. Nissen and Jenkins [47] reported that five of eight chimpanzees responded more predominantly on the basis of color rather than size. The relative efficacy of one cue or the other depended on the absolute size difference. It is possible that by magnifying size and form differences and reducing the color differences between the stimuli, trends might be reversed. An intermediate position is probably the most defensible one: animals generally depend more on one type of cue than another, but not exclusively on a single cue.

Inasmuch as birds also have color vision, a comparison here would be especially interesting. Jones [26] has provided us with these data. He trained six Silver King pigeons to perform a discrimination involving color, form, and position. Later the same subjects were tested on single-dimension problems. The form discrimination was consistently the most difficult; color and position discriminations were equally easy.

Objects and Patterns. If the stimuli consist of such objects as an ash tray and an oilcan, they can be differentiated on the basis of their object quality. A pattern discrimination, on the other hand, involves such forms as squares or triangles painted or fastened on *identical* objects. Thus, two white plaques, on one of which is painted a circle and on the other a square, would constitute a pattern-discrimination problem. When monkeys were tested, discrimination of objects was consistently better than that of patterns.

Recent studies [70] have shown that monkeys do not discriminate as well between two "regular" patterns (or between two "irregular" patterns) as between a regular and an irregular pattern. "Regular" patterns have "good" gestalt, e.g., both possess symmetry.

At this point we may review our definition of objects and patterns. We said that patterns are painted or mounted on larger identical objects. This means that the borders (the edges that lie on the testing tray) of the two patterned stimuli are identical, whereas for objects the borders differ in color, form, or size. Is this border critical? Very much so, at least for monkeys. Klüver [29] observed that Java monkeys (a close relative of the common rhesus monkey) trained on a size discrimination between objects lost their discrimination when those objects were placed on identical backgrounds. Warren [70] found superiority in learning when the critical difference involved the borders rather than the central portions of the stimuli to be discriminated. Data collected for macaques [56] show clearly that color discriminations based on different perimeters of pattern stimuli composed of concentric rings are easier than those based on the more central portions of the patterns. The data demonstrate a gradient of discriminability along this dimension. It is possible that this effect accounts, in part, for the ease of discrimination between one regular and one irregular pattern, for in this case, similarity of contour is minimal.

Comparable data on nonprimate animals are meager. However, one study shows the same importance of the border for discrimination learning by rats [9]. Rats on a Lashley jumping stand tend to respond to the bottom edges of the stimulus cards.

The importance of the border is easy to understand. It represents the limit of the entity termed the object. If the test object is to be perceived as different from the ground (tray) on which it is presented, the border must be perceived.

Contiguity of Stimulus and Reward. The rapidity of discrimination learning is dependent upon the contiguity of stimuli to the effects following the responses. Using monkeys and chimpanzees, Jarvik [24] placed the discriminal cues (colors) in close association with the reward and punishment. Small pieces of bread were colored red or green with vegetable dyes. Some were sweetened and some were made distasteful by adding an extract of capsicum (red pepper) and quinine. The subjects were first given the sweetened or rewarding object which they always ate. Then they were given the negative object; they tasted it and invariably dropped it. No chimpanzee made more than two errors in twenty trials; no monkey made more than one error in twenty-five trials, despite the fact that four monkeys had never been tested before. (The chimpanzees had been tested previously by usual methods.) Other methods of testing for contiguity of the reward (food) and the colors (the cues) were used.

On the second day the monkeys were tested with red and green plaques over food wells. On the third day uncolored squares of bread, flavored the same way as the original colored breads, were placed in the food wells. Then a red transparent celluloid was placed over the positive white piece of bread and green celluloid over the negative white piece of bread. The pieces of bread were clearly visible and, of course, *appeared* red and green. On the fourth day small red and green squares of celluloid were pasted on the bread. On the fifth day these celluloid squares were laid about 1 millimeter in front of the bread. The results for the three naïve rhesus monkeys are shown in Table 8-1.

Table 8-1

Percentage Errors in Twenty-five Discrimination-learning Trials for Three Rhesus Monkeys

Day	1	2	3	4	5
Condition	Colored bread	Colored plaques	Transparent stimulus	Pasted stimulus	Adjacent stimulus
Subject 1	0	56	44	0	44
Subject 2	0	52	36	0	40
Subject 3	4	60	48	0	48

The results show that the animals could quickly see the relation between the reward and the relevant stimuli if cue and reward were spatially and temporally contiguous (days 1 and 4).

Contiguity of Stimulus and Response. In general, contiguity of stimuli to be discriminated and of responses aids learning. Gellermann [12] trained chimpanzees to discriminate between two stimuli pasted on the front of food boxes, the lids of which had to be raised to secure food. Efforts to learn were fruitless in the first 500 trials apparently because the necessary stimulus cues were hidden by the raised lids when the responses were made. At this point the stimuli were moved to a position adjacent to and on the same plane with the box lids. Under these conditions the apes learned to respond correctly in about fifty trials each. In another study [37] with monkeys, the same results were obtained: the closer the stimuli to be discriminated and the response, the better was performance.

Rats trained to jump *through the stimuli* in a Lashley jumping apparatus learn discriminations faster than if they jump through nondifferentiated cards located adjacent to the cue cards [77]. Apparently the effectiveness of contiguity of stimulus and response is not restricted to primates.

Number of Negative Stimuli. If in the simultaneous-discrimination method there is one positive and one negative stimulus, is discrimination better than if there are many identical negative stimuli? Results with cats [65] and with chimpanzees [45] indicate more efficient learning when several identical negative stimuli are used. Pastore [52] taught canaries to select the odd one of three stimuli. Although the birds had little preference for the odd stimulus, they learned to respond to it. Performance improved substantially when eight rather than only two identical negative objects were used. When many stimuli of one kind and only one of another kind are present, the single one apparently "stands out" as different from the others.

Similarity and Difference. If the odd stimulus stands out perceptually from the others, it means that the similarity or diversity of objects can itself be a cue for discrimination. Can an animal distinguish the homogeneous from the heterogeneous? Robinson [58] was able to train chimpanzees to select a board carrying two identical objects and to reject a board carrying dissimilar objects. Furthermore, this tendency generalized to new problems, showing that not only were the animals able to respond differentially to the two stimulus complexes, they were able also to use the sameness-difference relation as a cue.

In the discussion above we have examined what might be termed the static aspects of perceptual learning; that is, we have discussed the effects of factors created by the physical attributes of the presented stimuli (color, size, form) and by the contiguity of the to-be-discriminated cues and the rewarded responses. We have seen that if the difference between the stimuli involves color (hue, brightness, or saturation), learning is more rapid than if the difference involves only size. Similarly, if complex stimuli involving both color and size differences are discriminated and subsequently the number of possible cues is restricted to either a color or a size difference, performance on the size difference is inferior to that on the color difference. In this sense, color cues are more distinctive than are the size cues. Distinctiveness, at least according to the gestalt psychologists, is determined by the laws of perception and by the innate make-up of the organism.

Acquired Distinctiveness of Cues

Is it possible, however, to alter the relative distinctiveness of cues by special training? From the data of Lawrence [34], such would seem to be the case. He trained a group of rats on a black-white discrimination problem, using the simultaneous procedure, in which the rewarded stimulus was responded to irrespective of its location. He later trained the same animals on the black-white discrimination problem, only he then used a different training method. When the black cue was presented alone, food was located on the right; when the white appeared, food was on the left. A different discrimination is required on the last training than was required on the first. Locus of the food was irrelevant in the first; in the second it was significant. Thus we might expect that what was learned in the first problem would be of no special benefit in the solution of the second. The results were not in agreement with this expectation: original training on the black versus white transferred positively to the second problem, even though it required quite a different stimulus-response relation. The trained rats solved the second problem utilizing the black-white differentiation effective in the first problem. The training had enhanced the distinctiveness of black and white cues and aided the animals even under the requirements of learning spatial cues. Such clear evidence for trainable cue selectivity in rodents had not been presented before Lawrence's work.

"Observing" Responses

Cues can become distinctive only if they become a part of the sensory field of the subjects. It is obvious that if an animal is to perform in a discrimination problem at levels better than chance, the stimuli to be discriminated must be observed. What does this involve? Attention? Or is it simply that certain areas of the visual field are more effective than others? As previously stated, if the stimuli are placed in a favorable position with respect to the animals' normal line of vision, learning will be rapid. Conversely, discrimination between two patterns may be based only on that portion of the pattern which is in a favorable position for observation. In the Lashley jumping apparatus, for example, rats tend to discriminate between patterns primarily on the basis of the lower or inner margins of the figures [29]. If the patterns are moved, new aspects of the stimulus field become critical.

In order to discriminate effectively between two stimuli, the animal may learn orienting and fixating responses of the head and eyes. *These orienting responses bring the relevant stimuli within effective visual range though they are not themselves directly instrumental in securing reward.* For example, Wyckoff [78] placed pigeons in a Skinner box where they could strike a single key. At the beginning of each trial the key was white. The "observing response" consisted of stepping on a pedal on the compartment floor. When this response occurred, the stimulus key was illuminated by either a red or a green light. Then, depending on the color, the appropriate discriminative response took place. The pigeon learned to depress the pedal and then to perform appropriately according to the particular color that appeared. By its own action, the bird changed its external field and thus aided its orientation to the new aspects therein.

LEARNING SETS

In our discussion thus far we have considered the manner in which a single or, at most, a few discriminations may be learned. Typically, the animal under investigation is learning his first discrimination problem of a particular type, i.e., the animal is "naïve." However, there are investigations in which animals are trained on many discrimination problems. For example, Harlow [16] gave a group of eight monkeys not 1, not 2, but 344 object-discrimination problems using 344 different pairs of stimuli. Each of the first 32 problems was 50 trials long, and an average of 9 trials was given on the last 112 problems. Once a monkey had gone through the requisite number of trials on a given problem, he never saw that problem again.

Figure 8-3 shows the percentage of correct responses made on each of the first six trials of these discrimination problems. The bottom curve shows the performance on the first eight problems; the highest curve, the last problems. This figure shows that the monkeys progressively improved in their ability to learn these discrimination problems. This progressive improvement, this "learning to learn," Harlow called the formation of "learning sets." From the data presented in Figure 8-3, it can be seen that after monkeys are well trained, they can solve such discrimination problems in a single trial; e.g., in the last block of problems the animals made 97 per cent correct on the second trials of the problem. In other words, the solution of each new discrimination was not preceded by several trials at chance level. The animal immediately discriminated the necessary cue and responded correctly.

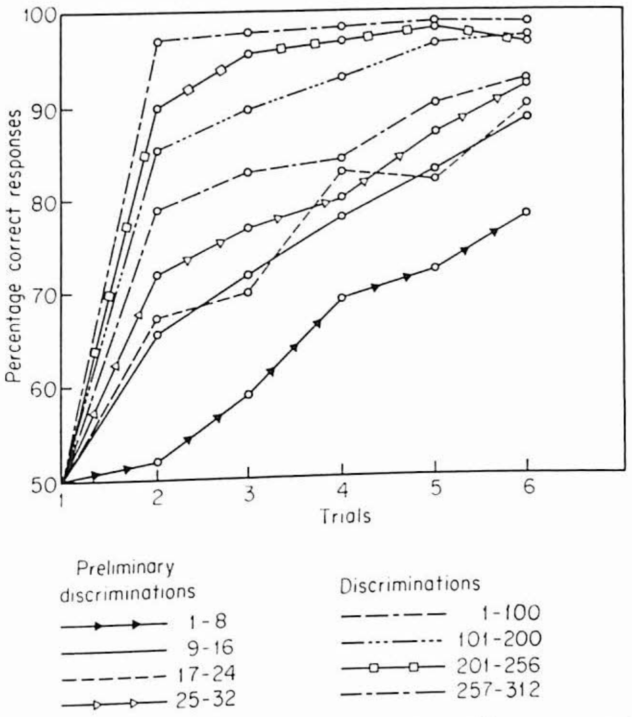

FIG. 8-3. Successive learning curves in the formation of learning sets by monkeys.

Within the past few years several species of animals have been tested in similar situations. Hayes, Thompson, and Hayes gave extensive training to five chimpanzees on the apparatus illustrated in Figure 8-1 and demonstrated highly efficient learning sets with this species. It is their impression, "Man, chimpanzee, and monkey probably differ little in their abilities to acquire learning sets of this type" [20, p. 104]. (These authors doubtless were referring to the Old World macaque monkey, the kind tested by Harlow.)

In several laboratories investigators have tested other species of monkeys and carnivores: the golden spider monkey of Central America, the cinnamon ringtail monkey [61], squirrel monkeys [41], and marmosets [40]. Similarities among the procedures are great enough so that we may plot all data on a single graph. The results are clear. Marked differences in capacity to form learning sets exist among species of the primate order: rhesus monkeys at the top and marmosets at the bottom. The superiority of the rhesus (Old World) monkey in comparison with the spider (New World) monkey is in line with the usual greater capacity of the Old World over the New World monkeys. Moreover it is unlikely that any other of the New World monkeys would surpass the spider. In noting the above differences in the formation of learning sets among the species, it would be a mistake to infer that no overlap exists. Superior individuals in one species may equal or surpass the inferior ones of a "higher" species. The above differences are *quantitative*, not *qualitative*.

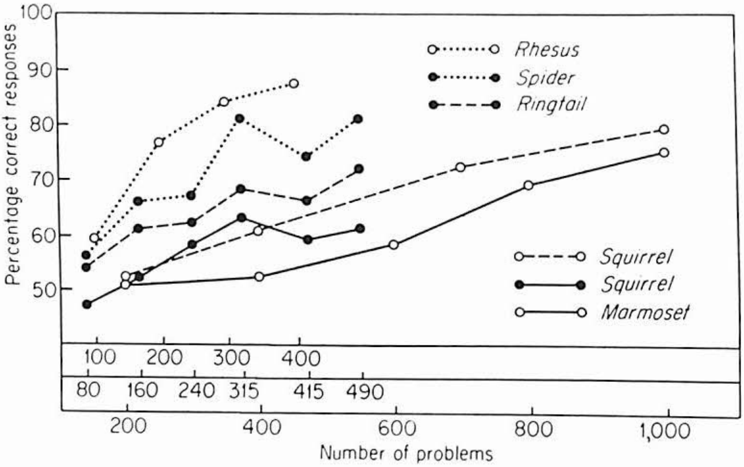

FIG. 8-4. Formation of learning sets in New World and Old World monkeys. Values along the horizontal axis are spaced so that the curves may be compared directly. Points on the abscissa are midpoints of intervals. Note the close agreement between the two curves for squirrel monkeys, despite the fact that they represent data from two different laboratories.

The good performance in the above studies of the rhesus monkey and the chimpanzee does not, however, fix the upper limit, nor does that of the marmosets fix the lower limit of learning-set performance. Preschool children easily surpass the best of the rhesus monkeys when tested under similar conditions [16]. And a lower level of learning-set performance is illustrated by data from two species of carnivore, cats [73] and raccoons [62]. We can see from Figures 8-5 and 8-6 that these two species of carnivore differ relatively little, with the nod going to the cat. (Since the raccoons were wild when trapped and never became tame enough to handle as pets, differences in performance may reflect tameness and domesticity rather than capacity.) The differences between the performances of these carnivores and primates are great. They may be explained in part, but only in part, by the absence or near absence of color vision. Other factors seem to be involved. That proficient learning sets depend on more than discrimination ability is seen from an additional fact. Monkeys that have suffered surgical damage to the frontal lobes of the brain solve difficult pattern-discrimination problems as readily as do normal monkeys, yet our unpublished data reveal that these same monkeys show inferior performance on learning-set problems.

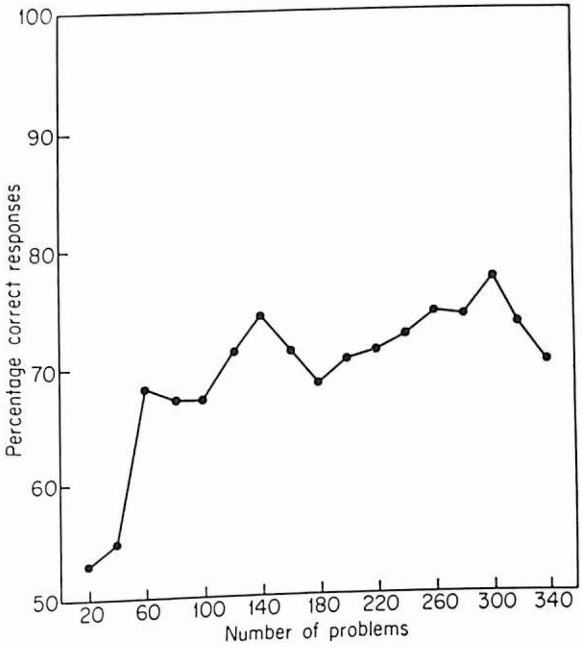

FIG. 8-5. Learning-set performance in the cat. The percentage of correct responses on trials 2 to 10 is plotted for successive blocks of problems.

Factors Determining Proficiency of Learning Sets

Now that we have seen how the learning-set performance arranges a variety of species in a somewhat orderly fashion and how it discriminates between normal and brain-damaged monkeys, we ask how it occurs. To answer that question two opposing sorts of explanations may be sought. We might ask why performance is so poor at the beginning of discrimination training, or, conversely, we might ask why performance is so good at the end. Explanations of the first sort assume that the "natural" performance would be nearly perfect at the beginning but that something interferes with the discrimination. Explanations of the second sort imply that the "natural" performance of a naïve animal is near to the chance level and that because sophisticated animals have acquired new skills they can solve new problems with utmost speed. It has been suggested, for example, that the formation of learning sets is akin to learning by insight. If so, it deserves the most careful scrutiny.

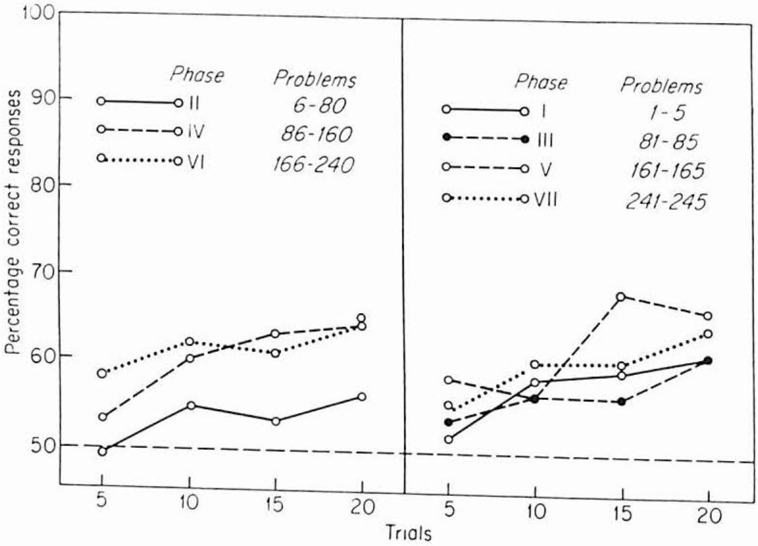

FIG. 8-6. Learning-set performance in the raccoon. Data in the left panel denote performance on successive blocks of seventy-five problems (twenty trials per problem). Data in the right panel show performance on problems learned to a criterion.

Interpretations of learning-set phenomena might proceed along one or more of the following lines: (*a*) the *supporting-habits* hypothesis suggests that discrimination is very rapid but that successful performance depends in part upon the acquisition of certain supporting habits which are learned more slowly. A good example of such a supporting habit would be the "observing response" described above. (*b*) The *interfering-habits* interpretation similarly assumes that there is rapid or even immediate discrimination but that proficient performance is not revealed until after the elimination of incompatible responses, such as position habits interfering with correct responses.

We note that both these last two interpretations minimize the significance of the characteristics of stimuli used and the interrelations among sequences of stimulus objects, and both assume excellent "natural" discrimination. Two contrasting theories are now presented which emphasize stimulus characteristics as critical in the rapidity of acquiring a learning set. (*c*) The *transfer theory* implies that intraproblem discrimination is acquired slowly *unless* the stimulus aspects of a given problem have already been differentiated through experience with similar stimulus aspects of previous problems. Illustration of this theory is Lawrence's study indicating that "distinctiveness of cues" can be acquired and transferred to later learning. (*d*) The *stimulus-independence theory* suggests that the successive problems become more readily differentiated from each other since responses to a particular problem are *not* eventually transferred to succeeding problems. In other words, it is assumed that there is more specificity and less generalization of *response* as training proceeds on successive discriminations.

No conclusion can be drawn concerning the "best" theory for learning sets. Only a start has been made on a complete analysis of learning sets. However, some data have been gathered which at least support one of these theories, the interfering-habits interpretation. Monkeys bring many biases, erroneous or irrelevant response tendencies, to each problem. Although these tendencies are extinguished to a greater or lesser degree within any problem, depending on the stage of training, they nevertheless return at nearly full relative strength on the first trial of the next problem. If the animal learns, he apparently becomes more and more proficient at suppressing interfering response tendencies. Examples of such interfering tendencies which are suppressed are position habits and tendencies to explore the other stimulus even though the first responses have been to the rewarded stimulus.

Perhaps the most significant interfering tendency is that due to marked preferences and aversions for certain stimuli. These preferences may be caused by extralaboratory factors or they may be based on superficial similarities between successive problems. As a result, the naïve animals get all the trials right on some problems and all the trials wrong on others. This is in sharp contrast to what usually is observed when a new problem is introduced at the beginning of the training and response preferences are *not* present.

There is some reason to believe that the perseveration tendency to respond to certain stimuli and not to others is especially important in lower animals and that it persists through many problems. Recent data [73] show that the tendency is much more persistent (extends through more problems) in cats than it is in monkeys. Data gathered for the raccoon show that this tendency persists through several hundred problems. A detailed analysis of contributing factors has revealed that because carnivores are so stimulus-bound they form learning sets much more slowly than do primates.

Facility in the formation of learning sets has proven to be one of the most sensitive tests yet devised for measuring problem-solving ability in different species. No other test has so consistently and so meaningfully arranged the species. This does not mean that comparison among species in respect to discrimination learning does not reveal phylogenetic differences. On the contrary, such comparisons are still equally valid. But, as we have seen, the succession of problems increases the complexity of factors determining changes in performance.

OBSERVATIONAL LEARNING AND IMITATION

Animals at all, or almost all, phylogenetic levels can modify their behavior on the basis of their own experience, i.e., they can learn. In the typical learning study, the animals are aided by reward or punishment for their responses. But can animals profit from observing the rewarded and nonrewarded, or the punished, responses of other animals?

Two different procedures have been used in studying such observational learning. In one procedure, an animal known as the "demonstrator" executes a response in some kind of apparatus and thereby conveys "information" to a second animal, the "observer," who, when tested later, shows whether he has learned from his observation. In the second procedure, an animal while, or after, observing another perform an act, attempts to duplicate ("copy") that act. In the former case there is no necessity for formal similarity of the responses of the two animals, whereas in the second case, similarity of the acts is crucial.

Unfortunately, in few investigations has the above distinction been maintained. The same descriptive terms have been used, the most common of which is "imitation." A few decades ago, "imitation" was thought to be an instinct characteristic of many species. The comparative psychologist attempted to determine the lowest phylogenetic level in which this instinct appeared. Today it is recognized that "imitation" includes several varieties of behavior, each of which is a function of different factors. The present aims are to differentiate, analyze, and explain the various kinds of behavior affected in some way by the observation of one animal by another.

In an early study, Thorndike devised a special test situation in which one bird, the observer, had an opportunity to imitate a skilled demonstrator. In these first experiments on imitation, Thorndike used the problem-box method. The bird had to escape from an enclosure by performing some act. An illustration follows for chicks: "No. 64 learned to get out of a pen by crowding under the wire screen at a certain point. There was also a chance to get out by walking up an inclined plane and then jumping down. No. 66 was put in with 64. After 9 minutes 20 seconds, 66 went out by the inclined plane, although 64 had in the meantime crawled out under the screen 9 times" [66, p. 51]. Thorndike also tested dogs, cats, and monkeys. With this last animal, he himself served as demonstrator. Thorndike denied evidence for imitation in all animals he tested. Other investigators found some evidence of imitation. Kinnaman claimed that a female rhesus monkey imitated a male monkey in opening the catch on a door of a puzzle box [28].

Results supporting imitation in problem-box learning were also obtained from cats [21]. Five problems were used, in each of which one animal performed on the problem while another could observe. The simplest problem involved a turntable bearing food which had to be rotated by the cat to secure the food (Fig. 8-7). The most difficult was a pedal-door arrangement. Some animals observed during the entire learning period of the demonstrator, and other animals observed only the last, the most skillful trials of the demonstrators. In general, scores for observers were consistently better than those for nonobservers. Also, animals that observed for all trials solved the problems faster than those observing only the skilled performances. The investigators concluded that either prolonged observation or observation of errors was beneficial to learning.

Warden and Jackson [69] introduced the *duplicate-cage method* to test for imitation. Two problem boxes, side by side, were used. One contained the demonstrator, the other the observer. As soon as the demonstrator solved his problem, an identical problem was revealed in the observer's cage. This apparatus, which permitted testing immediately after demonstration, produced imitative responses in 46 per cent of all tests (six tests on each of four problems for fifteen monkeys).

How did imitation occur? Crawford and Spence argue that "in the problem-box test the activity of the demonstrator simply enhances certain aspects of the stimulus situation which the imitator later attacks in his own way. Since discovery of the locus of attack is usually the most difficult part of a problem-box test, the imitator often meets with quick success without need of specific copy, after beginning to manipulate the part last manipulated by the demonstrator" [6, pp. 133 to 134].

Following the report of Crawford and Spence, a number of factors affecting ease of discrimination learning have come to light. After it was shown that one-trial learning in monkeys could be made the rule rather than the exception by means of learning-set procedures, Darby [7] adapted the procedures to the study of observational learning. Two monkeys faced each other across a test board on which was a pair of stimulus objects. The demonstrator was allowed one trial on the problem. This

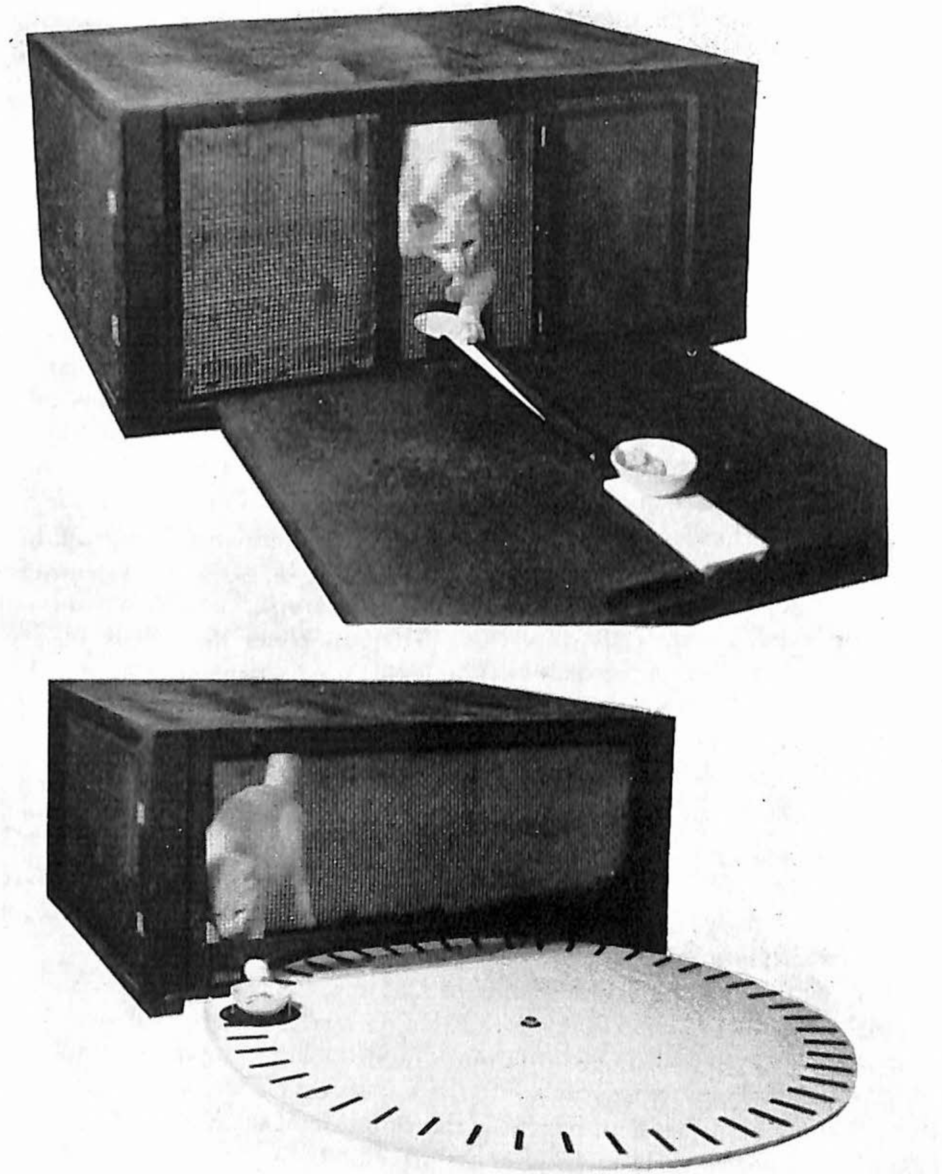

FIG. 8-7. Two tests used by Herbert and Harsh to study observational learning. Animals were tested after they had observed another perform the task.

demonstration was observed by the second animal, which was then tested. The animals were naïve at the beginning of the experiment, but they acquired much skill in discrimination learning during the series of 500 problems, as is shown in Figure 8-8. The data are plotted in fifty-problem blocks. The solid line with filled circles shows the performance of the observer's first choice. Improvement in performance took place throughout the entire 500 problems until a level of 75 per cent correct was attained. Both the demonstrator and the observer were given second trials. Performance on these trials is also shown in Figure 8-8. The difference in favor of the observer in the latter part of the training is small though consistent. The demonstrator's second-trial performance gives an idea of typical learning-set accomplishment. (The demonstrator had a chance to watch the observer's test trial, so this curve actually represents performance after both a choice trial and an observation trial. Hence it is likely to be a slight overestimation of performance.) If the difference favoring the observer's second test trial is real, it suggests that learning is better when observation precedes the test rather than the other way around.

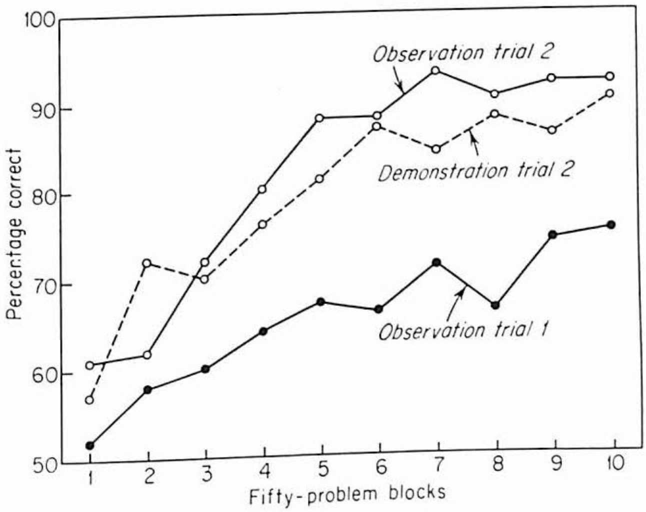

FIG. 8-8. Acquisition of observational-learning performance by monkeys. The line with filled circles denotes performance on the first test trial of the animal that had an opportunity to observe one demonstration trial. Performance by the demonstrator on that one trial was exactly 50 per cent correct. Curves with open circles refer to second-trial performance of the demonstrator and the observer.

Darby further analyzed his data to determine whether the observer went to the object first selected by the demonstrator (as expected in "stimulus enhancement") or whether it went to the rewarded object. The results showed that the animals had no significant tendency to select the object first chosen by the demonstrator; instead, they preferred the correct object, thereby showing that they made use of the information concerning the food-object relationship gained during the demonstration.

In a subsequent study on observational learning with experienced monkeys, Michels [39] trained the observers to do one of the following: (*a*) choose the object selected by the demonstrator, (*b*) choose the object *not* selected by the demonstrator, or (*c*) choose the *correct* object as defined in Darby's experiment. The results confirm and extend Darby's: first-trial performance significantly better than chance was obtained in every case. These data clearly show that the rhesus monkey in an object-quality discrimination situation can profit from the successes and the failures of the demonstrator.

That the demonstrator need not be of the same genus as the observer is seen from some data gathered by Harlow [15] in a slightly different context. He trained monkeys for "zero-trial" discrimination by presenting the discriminanda with an accompanying sign stimulus (showing food over the correct object or merely tapping it). He found that either of these procedures facilitated learning of the discriminations. A second method, involving alternation of reward between the two members of a single pair of stimuli, again resulted in highly efficient performance. From this experiment it would appear that the demonstrator may be any one of a variety of species. It also would appear that one function of the demonstrator, as far as observational learning of this type is concerned, is to reveal the relationship between the reward and the associated stimulus. (If this is true, perhaps the function can be accomplished without benefit of a demonstrator which in any way resembles the observer.)

A different definition, discrimination, species, and a different temporal sequence were employed by Miller and Dollard [42]. They trained rats to follow a leader through a T maze. The leader was trained to make a black-white discrimination. Two groups of observers were used. Some were rewarded if they followed the leader through the choice point; others were trained to turn in the opposite direction. Miller and Dollard called the response of the former group "imitation" and that of the latter group "nonimitation." The results, as shown in Figure 8-9, indicate that both responses are readily learned. These authors believe that all learning occurs when, and only when, a drive is reduced. "The learner must be driven to make the response and rewarded for having responded in the presence of the cue" [42, p. 2]. The secret of training to imitate is to reward all imitative responses, or so they claim.

Mowrer, in his study of training birds to "talk," agrees that rewarding the correct response will increase the probability that it will be repeated, but how does one ever get a bird to say a word in the first place? Once that happens, the rest is easy. According to Mowrer's hypothesis, a likely chain of events follows: First you must get the animal to like you; you do this by first starving the animal, then feeding him. "As a result of this procedure all the stimuli which are incidentally associated with the person of the trainer—particularly his appearance and the noises he characteristically makes—take on positive sign value. Soon the bird reaches the point at which it is obviously 'glad to see' and equally 'glad to *hear*' the trainer" [43, p. 580]. The learning of this affective response is presumed to occur through sheer contiguity. The second stage, according to Mowrer, goes as follows: "Since the appearance of the trainer has, by the process just described, taken on secondary reward value, we have every reason to suppose that, if the bird could it would reproduce the visual stimuli associated with the trainer" [43, p. 581]. Obviously the bird cannot do this for visual stimuli but it can for auditory stimuli if it is one of a variety of "talking" species. Now, if one of the sounds happens to resemble, even slightly, one of the trainer's sounds, that sound will, by the principle of generalization, have some secondary-reward value, and the response involved in making it will be somewhat reinforced. Mowrer refers to this process as *autistic* learning since the reinforcement is self-administered.

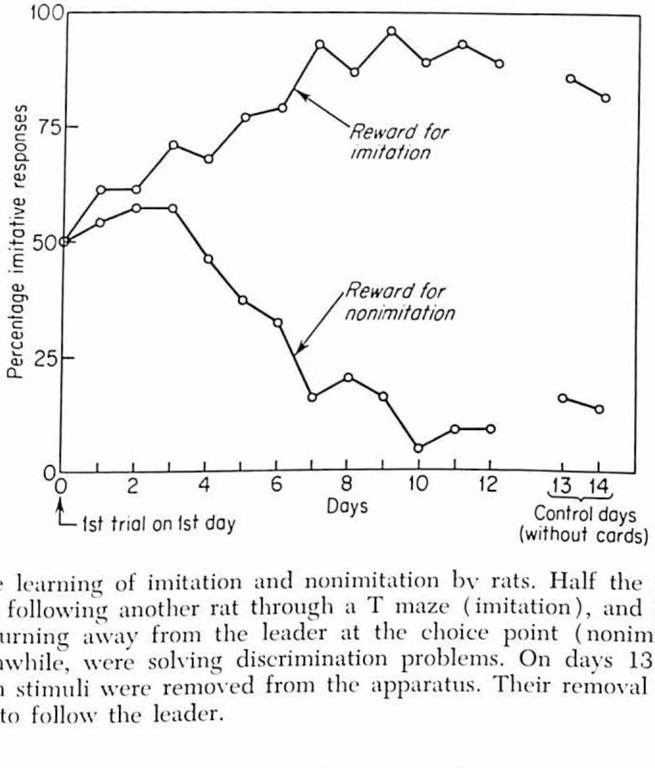

FIG. 8-9. The learning of imitation and nonimitation by rats. Half the animals were rewarded for following another rat through a T maze (imitation), and half were rewarded for turning away from the leader at the choice point (nonimitation). The leaders, meanwhile, were solving discrimination problems. On days 13 and 14, the discrimination stimuli were removed from the apparatus. Their removal did not alter the response to follow the leader.

However interesting the Mowrer theory or the theory of Miller and Dollard may be, the procedures they employ are such as to obscure or make irrelevant the observer's perception of what happens to the demonstrator as a consequence of his action. In the studies cited [42, 43], the observer cannot perceive whether the demonstrator is successful after certain acts and not after others. Rather, in Miller and Dollard's experiment, the rat called the imitator is learning that a reward follows his own response to the stimulus presented by the moving demonstrator. Thus the action of the leader rat only serves as a sign or cue stimulus to evoke a rewarded response from the learner. Any similarity of the response to that of the demonstrator is coincidental. It is questionable whether this learning should be called imitation. Assume, for example, that the learner was rewarded for merely following (or not following) a moving white light into one path of a maze. Would such a study be one of imitation or simply of discrimination?

There are situations, however, where the observer can perceive the significant relationships among certain aspects of the stimulus field, certain responses, and certain behavioral effects after the action of the demonstrator. In such situations the observer has the opportunity to *infer* that such behavioral effects would follow if he responded in a similar manner. That an observing animal might make such an inference would be at least supported if he showed one-trial learning after being given an opportunity to use the "information" gained during the observing period.

In the above discussion the emphasis was on those studies in which a demonstrator's behavior was directed toward obtaining a reward. Sometimes the action of an animal is to avoid a noxious stimulation. Can an observer, watching a trained animal, learn more quickly how to avoid harmful effects? Brogden [1] provided an opportunity for dogs to imitate in an avoidance-conditioning situation. A pair of animals was taken to the conditioning room. Both members of the pair were restrained in conditioning frames in such a way that one animal could see the other. The demonstration animal was then conditioned to withdraw his leg from a plate to avoid shock. Brogden found that not only did the observing dog fail to imitate the conditioned animal, it also failed to learn more rapidly when conditioned later. However, collected data [55] show that monkeys can learn something of the avoidance situation by watching another animal learn. Monkeys which had observed another learn to leap over a barrier in a double-compartment box whenever a light came on subsequently learned the response faster than did control animals. Whether the difference in results is due to differences in species or procedure is unknown.

Recently the Hayeses [19] raised a chimpanzee, Viki, in their home. They investigated her imitative ability along with that of a cage-reared animal and that of four children under three years of age. They observed many instances of imitation while Viki played. At about sixteen months of age Viki imitated a number of household tasks as performed by Mrs. Hayes. A fairly complete act of putting on lipstick was observed. Many of Viki's imitations occurred some time after the original demonstration.

Subsequently the Hayeses tried to establish a set to imitate. They wanted her to learn to imitate a response on the command "Do this." Seventy items were tried, of which many were too difficult for her to execute. For example, Viki would not close her eyes but did adopt the pseudosolution of putting her finger to her eye, which caused it to close. Figure 8-10 shows Viki imitating a photograph of herself. Viki was also given a series of problems to solve, such as the stick-and-tunnel problem. She solved this problem in about 30 seconds after the second demonstration. The children performed about as well as Viki did, whereas the cage-reared chimpanzee was decidedly inferior.

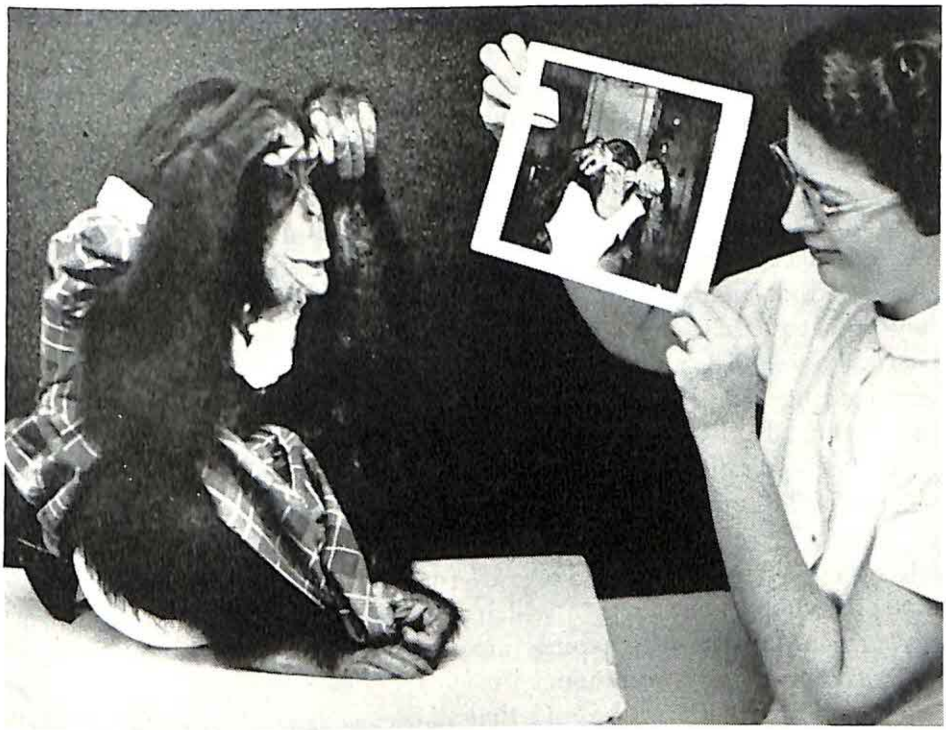

FIG. 8-10. Viki imitating a photograph of herself.

It is abundantly clear that the chimpanzee can and does imitate, immediately and after a lapse of time, in the widest sense of the term. Furthermore, the chimpanzee can learn to perform new copying responses upon command.

In a previous section we discussed discrimination learning and the factors upon which performance depends in each instance. Performance on any trial can be directly related to the animal's prior experience with reward. Thus the response on trial 2 of a problem is determined to a great extent on whether or not the animal obtained reward on trial 1. In the observational learning problems discussed in the present section, no such simple relationship can be found, for under these circumstances learning takes place even if a second animal gets the reward. Although it is not known whether or not rodents and carnivores can make systematic corrections for the erroneous responses of the demonstrator, it is clearly established that monkeys can if the problem is presented in such a way as to make use of the principles discussed in the early part of this chapter. Not only is there a decreased dependence on reward for learning in these animals, but evidence is at hand which points to the role of inference in determining the monkey's response.

Inferential imitation is to be distinguished from imitative copying behavior, in which emphasis is placed on duplicating an act in its form if not in its aim. Gradations in complexity of behavior are evident here also, and it is likely that the fundamental behavioral mechanisms differ also. Consider that kind of (imitative) behavior exhibited by birds when they repeat in their songs phrases from tunes whistled by the milkman. Thorndike, in 1898, wrote, "Now if a bird really gets a sound in his mind from hearing it and sets out forthwith to imitate it as mockingbirds are said at times to do, it is a mystery and deserves closest study. If a bird, out of a lot of random noises that it makes, chooses those for repetition which are like sounds he has heard, it is a mystery *why*, though not as in the previous case a mystery *how*, he does it" [66, p. 47]. The kind of imitation described by the Hayeses for chimpanzees is clearly of the first sort, whereas the kind in which one rat tracks another down a runway or the kind in which birds are trained to "talk" represent Thorndike's second type of imitation.

Summarization. It can be said that there are several ways by which a demonstrator serves the observer or learner. First, the action of the demonstrator may be merely a sign or cue to which a rewarded response (by the learner) is associated. This was illustrated when Miller and Dollard trained rats to respond to a moving maze-wise animal (as a stimulus) and to go through the maze.

A second way in which the demonstrator serves the learner is by permitting the latter to observe the place or locus in the external field where the correct responses must be made. This was illustrated in Harlow's study in which he, acting as the demonstrator for the monkeys, tapped or held food over the correct place. In this manner, or by other means, the demonstrator may simply *enhance* certain places, or aspects of the stimuli, which later the learner responds to in his own way, often by trial and error. Since the determination of the locus of attack (place to respond) is often the most difficult to achieve, such a service by a demonstrator may lead to very quick learning.

A third way by which a demonstrator may serve the observer is by performing the rewarded response. In the experiment described in the preceding pages, cats were aided by seeing the demonstrators' performance. However, being given an opportunity to perceive wrong responses was also found to be an aid; so their imitation was not simply copying a response.

A fourth aid of the demonstrator is to permit the learner to perceive the relations between certain stimuli and the rewarded responses. Assume the demonstrator's responses to a particular stimulus are followed by consumatory responses (eating) and that another response to that stimulus is not followed by eating. If this sequence is clearly presented, then the animal, at least on the level of the rhesus monkey, can profit immediately from the successes and failures of the demonstrator. How this occurs is not known, but it is possible that there is an inference by the observer, used later in this performance. The degree of previous experience of the observer in solving problems is significant in the use that he can make of demonstrations.

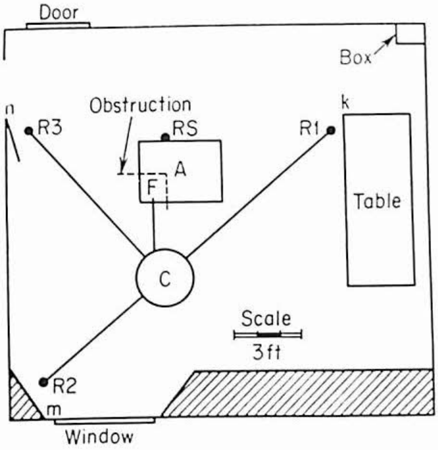

Fig. 8-11. Arrangement used by Maier to study "reasoning" in the rat.

REASONING

The studies of Darby cited above show clearly that primates are capable of combining two disparate experiences into a single reward-securing act, i.e., to reason. In the Darby experiment, the observing animals learned that when presented with two objects, one always covered food (experience 1). They also learned more or less efficiently which of the two objects covered food for the demonstrator (experience 2). When tested, the animals had an opportunity to combine these experiences to secure reward.

This definition of reasoning is neither new nor applicable solely to primates. Indeed, the first person to exploit it extensively did so with rats [35]. Figure 8-11 shows one of Maier's experimental situations. Next to table *A* in the center of the room is a ring stand *RS* which serves as a ladder by which the rats can go from the floor to the table top and back again. One corner of the table, *F*, is fenced off. During preliminary training the rats are given the freedom of the room for several days in which they explore the room thoroughly. This provides experience 1. Then the second table *C* is added, which is connected to point *F* by means of a pathway. Three other pathways also radiate from *C*. They terminate at ringstands *R*1, *R*2, and *R*3, each of which also leads to the floor. With the addition of these new structures, point *F* of table *A* is now accessible from everywhere in the room. The rat is now placed at the base of *R*1, *R*2, or *R*3 and encouraged to ascend. It is further guided until it reaches *F*, where it now finds food. Training continues until the rat readily climbs the ringstand and runs to food. This is experience 2. The rat is tested by being placed at *A*, where it is confronted with the task of obtaining food behind the fence. It has learned the necessary part responses; can it combine them to accomplish that end? In summarizing the results, Maier and Schneirla report, "The typical behavior of the rat in this situation involves (1) a period of struggle before the cage; (2) running back and forth between the cage and the edges of the table; (3) descending to the floor by means of *RS;* (4) going directly to the ringstand it used in experience 2; and (5) proceeding up the ringstand and to the food" [36, p. 462].

DELAYED RESPONSE

One of the early definitions of "symbolic" or "representative" processes was the ability to respond appropriately in the absence of the external stimulus. Should an animal do so, he must be responding to one that he himself has supplied. To determine whether such substitute stimuli are used, animals are first trained to respond to a stimulus which "points the way" to a rewarded response. Later this stimulus is removed before the animal is permitted to respond. Then, after the delay period, response is allowed. For example, suppose that we show a caged animal that we are dropping food into one of two identical containers located near each other. After a delay of several seconds, we release the animal and observe whether or not he goes to the container with the food. (Darby's study on observational learning, which employed 500 distinct problems, fully qualifies as a delayed-response experiment, as do the other studies involving delayed imitation, because the information trial and the test trial are separated several seconds in time.)

After having established that a brief interval can be bridged without complete deterioration of performance, investigators have raised the question of how long an interval can be tolerated by the various species. With differing techniques, maximum delays can be extended to minutes, hours, or days with a variety of mammalian species. The data are highly variable, and no reliable and consistent ranking of the species is possible. The reasons for this are several. First, there is little reason to believe that a

2-hour delay is more "representative" than one of 30 seconds. A long interval may merely reflect the degree of original learning. Second, the activity pace differs widely from species to species. A long delay in a turtle would not mean the same thing as the same delay would to a humming bird or a monkey. Third, temperamental characteristics of the various species are markedly different, and animals differ widely in their ability to withstand frustration. Finally, animals that are curious about their environment are likely to become distracted during the delay interval. These last two factors may themselves be related to intelligence and phyletic level.

FLEXIBILITY

An important characteristic of intelligent or creative behavior is the ability to perceive things in new ways, to be able to shift from one mental set to another. Not only is this capacity of significance for classifying and reclassifying a collection of specific items, it is also significant for responding appropriately to several different kinds of materials. A characteristic feature of such a capacity is the integration of two or more mutually incompatible habits.

Because there are numerous ways to produce the opposite of flexibility, i.e., habit interference, it is convenient to classify the methods according to the number of simultaneous habits that have to be interrelated. The particular experimental methods are generally the same as those described earlier, a point which not only emphasizes the continuity of simple and complex behavior but also suggests that the kinds of factors which were important for discrimination learning are equally important now. It further suggests that these more complex processes can and should be subjected to detailed analyses comparable to those described earlier.

Discrimination Reversal

Tasks of this type begin as discrimination problems. After a predetermined number of trials, the reward shifts to the other object. If the shift occurs without warning, the animal primarily derives his cue from the information obtained on the first trial after the shift in reward. Cole [4] tested three pigtail macaques, one patas monkey from Africa, and one rhesus monkey on a single discrimination-reversal problem. Learning to reverse was accomplished in every case by a gradual elimination of errors.

Reid [53] attempted to determine the effect of overlearning on flexibility, i.e., on the ease of reversal of responses after reward was shifted to a new cue. He overtrained rats on a black-white discrimination. The group with the greatest overtraining learned the reversed discrimination

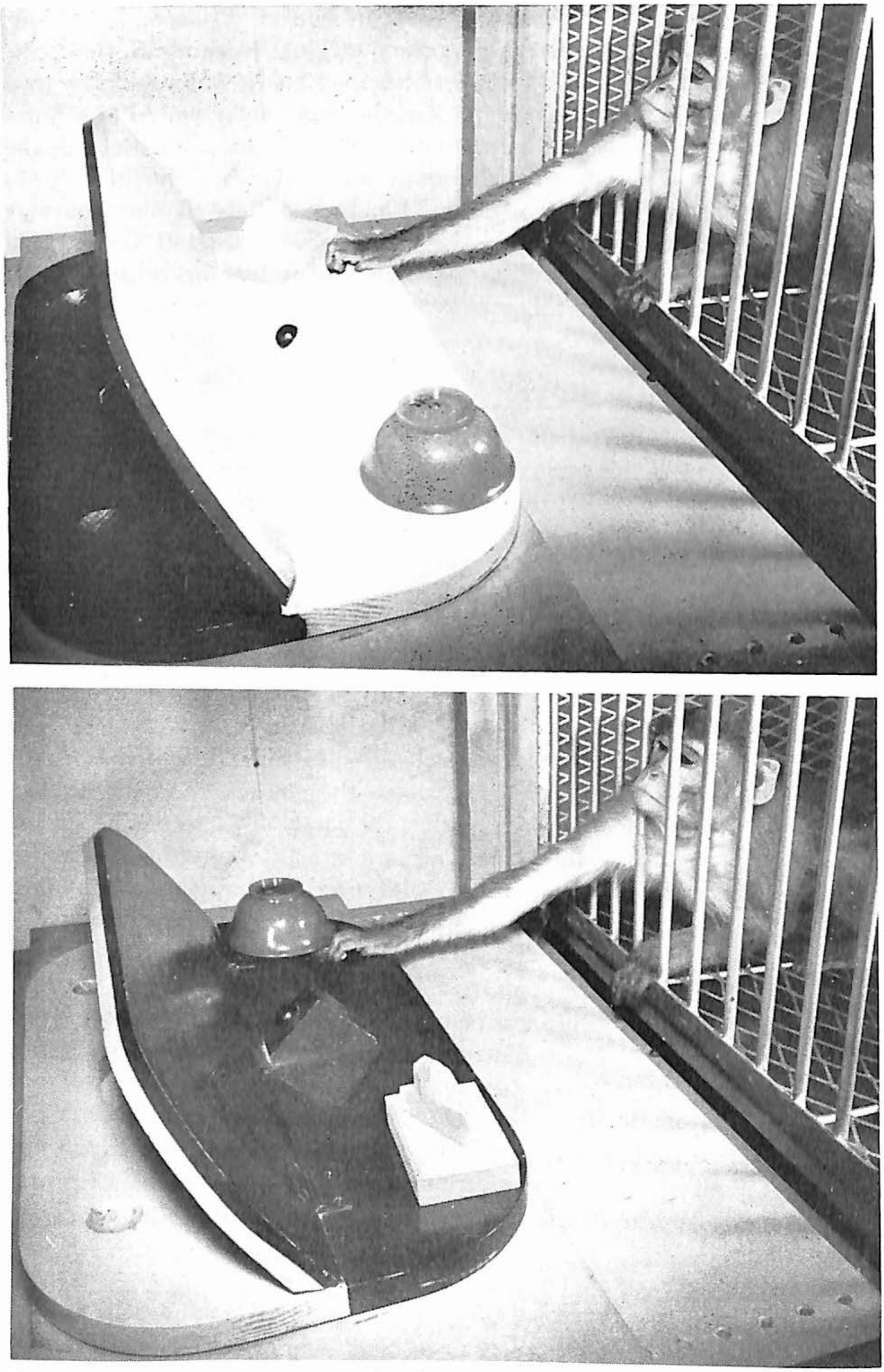

FIG. 8-12. Object correct on the dark bckground is incorrect on the light background.

most rapidly despite the fact that these rats also showed greatest persistence at first in going to the originally rewarded stimulus. When this group did begin to switch, it did so suddenly and almost completely. Groups with less overtraining reversed very slowly.

Harlow [17] trained seven rhesus monkeys and one mangabey (genus *Cercocebus* from equatorial Africa) on 112 discrimination-reversal problems after they had been trained on 232 discrimination problems. The shift in reward occurred after the seventh, ninth, or eleventh trials. At first the animals continued to choose the originally rewarded object for several trials even though it no longer brought reward. By the time they had completed the 112 problems, they were reversing their preferences in only one trial. (Many of the error-producing factors that operated in discrimination learning also were operative in discrimination-reversal learning.)

Another investigation [54] determined whether reversal could be cued by an external sign, such as by a change in the background color of the tray. The first 220 problems with rhesus monkeys all began as object-quality discrimination on a green test board, and after six or eight trials, the reward was shifted to the previously nonrewarded object. Concurrent with this shift was a shift in the board color from green to yellow. An illustrative problem is depicted in Figure 8-12. At the beginning of training, the shift in the color of the "ground" had no significance for the animals, but at the end of training, all animals shifted their responses without error when the "ground" changed. The monkeys were then tested on new sequences of "ground" or board colors. In the last phase of the experiment the animals were capable of performing discrimination reversals without error to color sequences they had not experienced previously. A *change* in color on the background became the critical cue, even though the particular colors involved were not themselves cues.

Unfortunately, data on subprimate animals are lacking. However, evidence from a wide variety of sources suggests that, similar to discrimination-learning sets, reversal-learning sets will be acquired more slowly by infraprimates than by primates. Reversal learning, with its emphasis on shifting of set, has been suggested as an accurate and sensitive test of ability, tapping at least one important aspect of intelligence [5]. Reversal learning deserves careful study and application to several species.

Successive Reversals within a Single Problem

Maximal interference comes if frequent reversals of the sign of a reward occur. The general conclusion is that the speed with which flexible performance appears in the repetitive reversals within such a single problem is not a direct index of species difference, for rats do as well, or perhaps better, than chimpanzees, and newts and terrapins do best of all [3, 8, 46, 60, 68]. One reason why the chimpanzees do so poorly is emotional upset. When frustrated, chimpanzees and also monkeys are likely to show deterioration of performance. It is likely that increased susceptibility to frustration and consequent performance deterioration is characteristic of higher animals. One is reminded, in this regard, of the finding that older children have more fears than younger children, the increase being accounted for strictly by the development of fears of the abstract, e.g., ghosts, the "dark," etc. [25].

Double-sign Learning

Conditional Discrimination. In the problems reported thus far the animal was usually required to respond to the relevant stimulus dimension and to ignore all other dimensions. In a size-discrimination problem, for example, the animal may be required to respond to the larger stimulus object regardless of its position, hue, or brightness. Some or all of stimulus dimensions are varied at random, and the animal must ignore these variations and respond to the single critical variation. One way of complicating the task is to designate the correct object by two dimensions rather than one. Thus, we might require the animal to select the larger object when the problem is presented on a light background and the smaller object when on a dark background. The animal must then respond to two cues: size of object and color of the test board.

Oddity. What is called the oddity problem requires the learning of a "double sign." Two pairs of identical stimuli are used in this problem. Only three of the four objects are presented on a single trial; two are alike and the third is different. The animal is required to select that object which differs from the other two. The task was described by Robinson [57], who trained a cynomolgus monkey from the Philippines to respond according to the principle of oddity. Meyer and Harlow [38] report that between 425 and 1,150 trials were required for their eight rhesus monkeys to learn problems of this type. Because some of the discriminations were of the more difficult type discussed earlier in this chapter, these figures underestimate the speed of learning.

The oddity problem is mastered very readily by chimpanzees [45]; indeed, it is not beyond the capability of the rat [76]. The canary, too, can solve it if conditions are right [52].

Matching. Complementary to the oddity problem is the matching problem. In the first form of the test, as devised by Kohts [31], several objects were held in a tray and a sample object was held in the experimenter's hand. The chimpanzee was trained to select that object on the tray which was identical with that held in the hand.

Nissen, Blum, and Blum [48] have discussed a variety of ways that the matching problem can be solved, and the student interested in this aspect of the problem should consult their work. More to our purpose is the conclusion they drew from a comparison of their work with other work involving chimpanzees and rhesus monkeys. Both species learn matching in 1,000 to 1,500 trials, with chimpanzees probably learning the problem faster.

Skinner has reported that "it is possible to get a pigeon to match a sample by reinforcing the discriminative responses of striking-red-after-being-stimulated-by-green while extinguishing the other two possibilities" [64, p. 213]. The pigeon is placed in a box containing three keys in a row. A colored light is flashed on the central key first, leaving the other two uncolored. When the bird pecks the central key, thereby forcing him to look at the sample, the two side keys are illuminated. Pecking the appropriate side key yields food reward. Skinner says, "Successful matching was readily established in all ten pigeons tested with this technique" [64, p. 214]. (Generalization of the problem to new colors, readily accomplished with Old World primates at this level of complexity of the problem [75], was not attempted.) Skinner reports that the bird will not respond correctly if all three keys are illuminated simultaneously. Instead, the bird will cease responding to the (nonreinforced) middle key. The experimenter must reinforce this observing response to keep it in strength. By way of comparison, Skinner states, "In monkeys, apes, and human subjects the ultimate success in choosing is apparently sufficient to reinforce and maintain the behavior of looking at the sample. It is possible that this species difference is simply a difference in the temporal relations required for reinforcement" [64, p. 214].

Two-sign problems are not beyond the capabilities of some nonprimate mammals. Because of the wide differences in procedures, direct comparisons among experiments are not possible; however, most of the data obtained thus far are in agreement with the usual ordering of species. When we come to three-sign and four-sign problems, we are most likely to exclude subprimates from the list of animals capable of solving them. The differentiation is likely to be even sharper and wider when generalization tests are conducted, for it is in generalization tests that we can be more nearly sure that the animal is solving the problem on an "if-then" basis rather than on the basis of learning several different problems under conditions of high negative transfer.

Higher-order Sign Learning

Animals that can be trained to do either the matching or the oddity problem can also be trained to do the other, since both are two-sign problems. If a third sign is introduced, the animal may be able to do both, each in turn, as denoted by this sign. Another possibility is to train the animal to perform oddity in two dimensions: odd form on one background and odd color on another background. The background color in this case serves as the third sign. Matching can be done in like manner. Tests of this type were adapted by Harlow [13, 14] from Weigl's test of abstraction [74]. This latter test consists of a dozen wooden blocks of three forms and four colors. The human subject is asked to sort the twelve blocks in several different ways that he himself must define. The task stresses the ability to shift set and has been found useful in the study of organic brain damage.

An illustrative problem involving the Weigl principle as applied to the oddity problem is presented in Figure 8-13. In this illustration the monkey is seen selecting the odd color on the light test tray and the odd form on the dark test tray. This is a superb example of acquired distinctiveness of cues. Both rhesus monkeys and chimpanzees [49] have been trained to solve problems of this type. Rhesus monkeys also show generalization of the principle [79]. It can also be said that not all rhesus monkeys or all chimpanzees tested succeeded; failures were found in both species under the conditions that prevailed. In view of the small number of subjects of both species that have been used, the presence of failures in both species, marked differences in laboratory settings as well as in previous test experience of the animals, no claims can be made for the superiority of either species.

Nissen attempted to determine whether there was a quantitative limit to the number of cues to which the chimpanzee can respond. He chose a mature, stable animal (Frank) that had previously undergone much training on successive discrimination reversals, to which we referred earlier, and was unusually well motivated to perform in the testing situation. Thirty-two stimulus objects were constructed, representing all possible combinations of five two-valued dimensions: size (large or small), color (white or black), form (square or triangle), margin (painted border present or absent), and peg (present or absent). In the first problem designated, only size was the relevant cue; the second problem involved both color and size. Simultaneous mastery of all sixteen pairs of habits involved all five dimensions. The training sequence, typical of most multiple-sign problems, was as follows: As soon as one problem was learned, training was started on the next. Progress in learning the new habit was usually accompanied by temporary deterioration of the old habits, since what was correct in the new context was wrong in the previous context.

Training was spread over a three-year period and involved a total of 17,740 trials. During the last fifteen sessions the chimpanzee made 71 to 100 per cent correct on the individual problems. The full impact of the complexity of the task may be felt in the following verbalized formulation

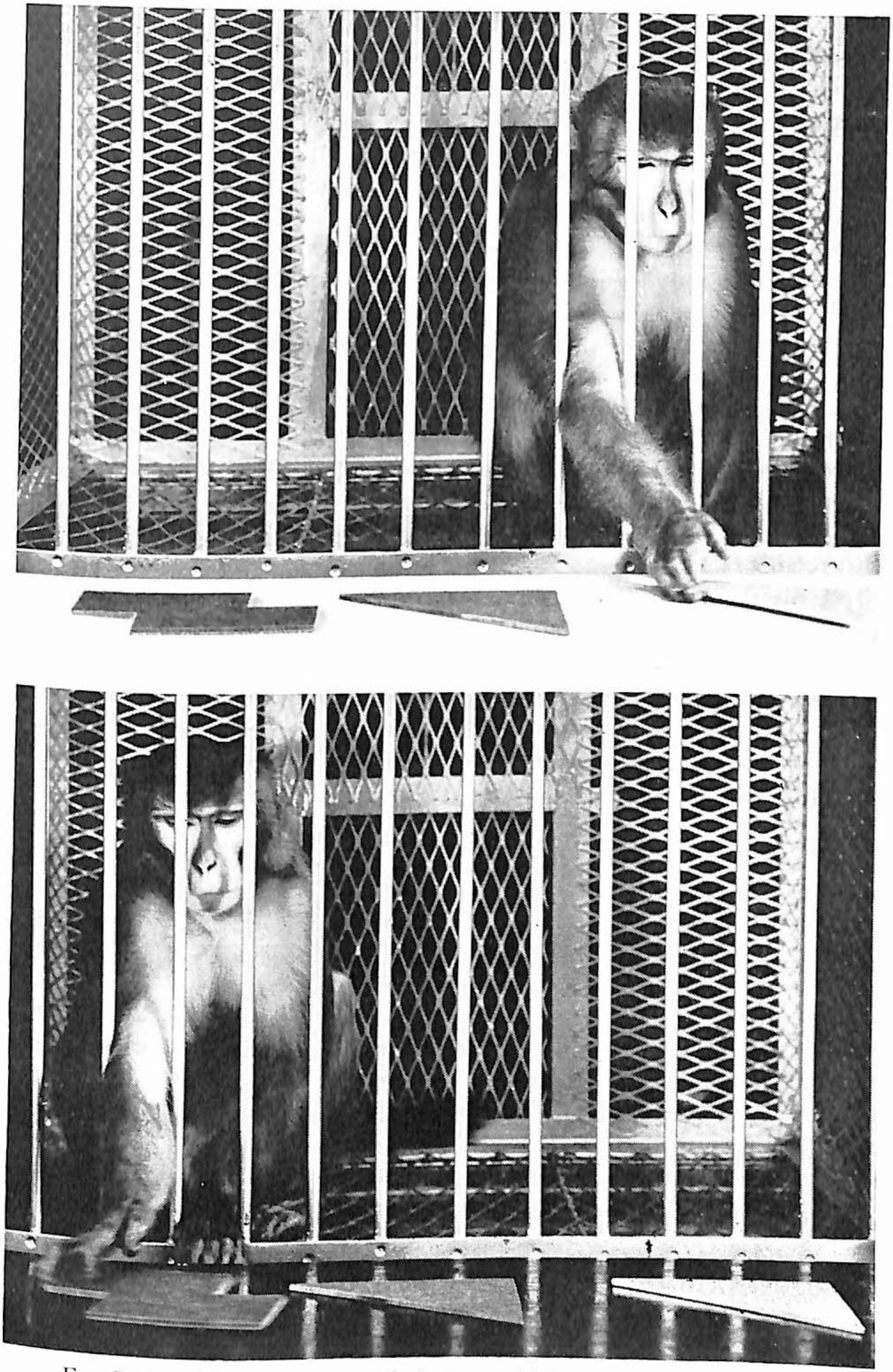

FIG. 8-13. Odd color correct on light tray; odd form correct on dark tray.

of the problem: "Of two white squares without margin or peg, the larger one is correct (habit I). Any pair differing from this one in an *even* number of respects—e.g., in color and shape (habit IV) or in color, shape, margin, and peg (habit XVI)—likewise demands response to the larger object, whereas any pair differing from this in an *odd* number of respects—e.g., in color (habit II) or in color, shape, and margin (habit VIII)—calls for response to the smaller object" [50, p. 15]. Nissen believes it highly unlikely that his subject utilized such a formulation; he believes it also unlikely that the chimpanzee simply learned sixteen independent configurations.

It would be a mistake to claim that five-sign problems define the upper limit of anthropoid capacity or that 17,740 trials will always be required. Since many of the factors operating in discrimination learning were discovered after these multiple-sign experiments were performed, we can appreciate the high levels of proficiency that have been demonstrated by primates. Also, we have a fuller grasp of the interdependence of complex processes on simpler processes. Because these complex tasks depend on proficient discrimination performance, precisely those factors which affect discrimination learning and the formation of learning sets will affect performance on multiple-sign problems. Furthermore, species which form learning sets inefficiently will also be expected to do poorly on generalized multiple-sign problems.

It is possible to place the entire burden of sign presentation on the stimulus objects themselves, as opposed to placing some of it on the tray. Consider the following schema:

$$\begin{tikzcd} w \arrow[d] & b \arrow[l] \\ W \arrow[r] & B \arrow[u] \end{tikzcd}$$

In this schema, four stimulus objects are represented, two of which are white (W, w) and two black (B, b); similarly, two are large (W, B) and two small (w, b). In each of the two "horizontal" and two "vertical" pairings, the rewarded member is designated by the arrowhead. A "horizontal" habit would involve a brightness discrimination whereas a "vertical" habit would involve a size discrimination.

INSTRUMENTATION

In most of the experiments described thus far, the physical arrangements were such that on the initial trial of each new problem the animal could not figure out the solution solely by surveying the situation. Instead, he had to arrive at a solution by noting which stimuli were consistently rewarded. The contribution of trial and error to eventual success is potentially great, and to avoid this, many tests have been devised which purport to measure insight. Typically, these tests involve the use of external objects as instruments to secure reward.

Patterned String Tests. In the simplest form of this test, a food morsel is placed just out of the animal's reach. Extending from the morsel to within reach is a string. The animal must pull the string to get the food. In this form, the test is solvable by birds. If crossing, nonrewarded strings are added, difficulty may be increased substantially. Only primates can solve the most difficult problems. Factors like those discussed in connection with discrimination learning are of equal importance in determining success on string problems.

Stick and Hoe Problems. Problems closely allied to those just described involve the use of a stick or a hoe to reach for and rake in a distant food morsel. Animals such as monkeys have good manual ability and can be tested on these problems. The test is easily complicated by increasing the number of rakes needed to solve the problem. That is, a short rake is needed to obtain a longer one and so on until the food can be obtained. Also, lateral separation between the rakes can be introduced. Several facts are well established about performances on these tests. First, the role of experience and acquaintance with sticks are important. In part this is due to maturation; in part it is due to learning. After all, the animal must learn about the stick's weight, length, and strength. Second, success and failure can be modified greatly by small changes in the spatial arrangement. For example, if the food on the table can be secured by merely pulling in the hoe, solution of the problem comes quickly. On the other hand, the problem is made immensely more difficult by putting the food a little to one side or beyond the hoe. Third, the initial success is frequently a chance affair and may arise out of play activity. Subsequent success may or may not follow quickly. Lastly, chimpanzees and cebus monkeys seem to be superior to other primates in these tests. Indeed, the cebus monkey may solve problems requiring up to eight rakes. These experiments, derived from those originally designed by Hobhouse [23] in 1901, have not been able to demonstrate that any species solves problems as complex as these solely on the basis of perceiving the relations between the objects. Instead, definite improvement comes with practice. In must also be said that the initial responses to problems are never completely blind.

Box Stacking. One of the most famous of all demonstrations of insightful behavior is based on the stacking of one or more boxes to form a structure on which the animal can climb to get to food hanging overhead. As the following illustrates, this type of activity requires the strength, agility, and manual skills of a primate. The test is conducted in a bare room, from the ceiling of which a banana is suspended out of the animal's reach. In the middle of the room, a few yards away from the banana, is a large box.

Let us follow Köhler's most famous subject, Sultan, as he tries to solve the problem. Upon entering the room he runs to the banana and leaps for it. He continues to do this repeatedly. Later he stops leaping and starts pacing around the room. Suddenly he stops in front of the box and moves it until it is directly beneath the food. Now he speedily jumps upon the box and reaches for the banana. Sultan will, on subsequent days, solve the problem very rapidly and without the preliminary false starts. Also, after extensive experience, Sultan can solve problems requiring more than one box by stacking them one on top of another [30].

Unfortunately, tasks of this type have not been subjected to the kind of detailed analysis that other tasks have undergone. We can be sure, however, that preliminary training on component skills and spatial contiguity of the rakes (or boxes), as well as other factors, will be of great importance. Furthermore, certain modes of motor responses characteristic of the animal or of the species will, if compatible with the required response, enhance the probability of success (and obscure for us the basis for solution). This point is emphasized by Schiller, who tested twelve chimpanzees in a room containing only boxes (no banana). All chimpanzees dragged the boxes around the room and "six of the animals actually stacked them and climbed on the tower, jumping upward from the top repeatedly, with arms lifted above the head and stretched toward the ceiling. For the human observer it was hard to believe that there was no food above them to be reached" [59, p. 186]. It is Schiller's thesis that the innate constituents of complex responses are not perceptual organizations, but motor patterns. This is a provocative thesis, and one which needs further investigations.

SUMMARY

The material discussed in the present chapter does not exhaust the work that has been done in the area of complex processes. Many other problems have been employed in the study of cognition, reason, and judgment and excellent treatments of these topics can be found in the writings of Maier and Schneirla [36], Heron [22], Harlow [18], and Nissen [51]. The student should consult the works of these authors.

Restricting our interpretation of phylogenetic comparisons to the data of the present chapter, we can state a few general themes which run through the entire set of data. First, not every test which ostensibly measures "intelligence" will neatly arrange the species on a ladder. There are several important reasons for this, one of which is simply that evolution did not yield such a stratification of the animals by any scale. Instead we see parallel evolution of several genera. The Old World monkeys, for example, have not been evolving any longer than have the New World. Both groups form independent radiations from ancestral stock. The same phenomenon occurs at most phyla. On the psychological side, also, the concept of intelligence, none too clear when applied to the measurement of human abilities, is not so definite as we would like it to be when applied to lower animals. Human intelligence includes the operation of several factors or abilities: spatial, numerical, verbal, etc., each of which contributes only partly to the over-all index. No unitary trait of intelligence has been successfully proposed. Similarly, no single trait will suffice for defining animal intelligence. Thus, ability to shift set is doubtless a component of intelligence; nevertheless, it is not the sole component, and a "pure" test of this ability will not arrange individuals or species in a descending order that will necessarily coincide with measures of other components of intelligence.

Another factor which enters to upset the psychologist's preconceived superiority of the "higher" animals is the restricted range of animals for which the test is optimally discriminative. Let us return to another analogy with mental measurement of humans to see this point more clearly. Arithmetic manipulations are undoubtedly components of intelligence, but a set of problems as simple as $2 + 2 = ?$ would not separate the bright from the dull, except at the lower levels of development. Errors on such items if committed by, say, high-school students would not reflect lack of intelligence. Perhaps some of the tests which purportedly measure animal intelligence do so only at restricted phyletic levels. Some tasks which fail to differentiate the primates from lower animals are precisely those which elicit frustration in these higher animals. The range and diversity of situations which provoke emotion are probably greater in these higher animals, and the lability of their emotions is greater. "Dogged" persistence in overcoming an obstacle is not a characteristic virtue of primates.

Another conclusion to be drawn from the data of this chapter is the continuity of the "simpler" and more "complex" processes, functions, and tasks. Psychologists who have devised tests to measure these functions tend to classify them in terms that are readily verbalized by humans. Thus, formal relations among the supposedly significant elements are presumably emphasized in these tests. As an illustration, the human concept of triangularity isolates the significant elements from the contextual through verbal cues. The more extensive the educational background of the highly sophisticated experimenter, the farther do his own perceptual processes deviate from those of the animal subject and the more difficult it is for the experimenter to appreciate the significance of supposedly irrelevant details. It may be that the perceptual processes of the uncivilized savage may be more similar to those of lower animals than to those of civilized, cultured persons. Triangularity in patterns is unchanged for the verbal human being, whether the stimuli are objects or patterns, large or small, or whether the goal is attached or separated from the stimuli. However, as we have seen, factors such as these are not irrelevant for the nonverbal animal, whose success or failure is certain to depend on them. Furthermore, the acquisition and skillful, facile manipulation of these simpler skills may permit a functional isolation and emphasis of the "relevant" aspects of the problem. These factors, then, must be taken into account in any adequate definition of animal intelligence. It is interesting to note that under conditions for optimal discrimination, such as in learning sets, species differences, even within the restricted range of the primates, are readily demonstrated.

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CHAPTER 9

Comparative Social Psychology

In the previous chapters of this book it has been convenient to assume that animals behave as individuals and that their actions have little effect on each other. Half a century ago this could have been taken as a valid assumption. According to the knowledge then available there were only two kinds of highly social animals, the social insects and man, and the social life of all other species was negligible. We now realize that all animals are social to some degree and that the effects of social factors often outweigh those coming from the physical and biological environments.

These new facts affect all branches of comparative psychology. At the present time we must take it for granted that any animal which is capable of behavior will show some degree of social interaction. This factor is always apparent in mammals, whose system of nutrition forces the development of a social relationship between mother and young even in the most solitary species. Less obvious but equally important social relationships are found in other types of animals. Consequently, any experimental study of animal behavior always involves a set of social variables, and the relationships of the animal to the rest of its species and to the experimenter are an essential part of the background of the experiment.

The kind of social relationship developed with the experimenter is particularly important in birds and mammals. At the Yerkes Laboratories the regular routine for experiments with chimpanzees includes removing the newborn animal from the mother and raising it largely with human beings. It is equally necessary to set up a social relationship between human handlers and dogs reared in the laboratory [52]. Otherwise, the animals become timid, unadaptable, and poor performers in learning situations. In fact, any mammal reared in a truly solitary fashion shows behavior which is quite abnormal for its species. Even in laboratory rats, the amount of handling and the age at which it is given may have considerable effect on behavior in experimental situations [35].

For these reasons, thorough study of the social aspects of behavior is a necessary basis for understanding behavior as a whole. In this chapter we are going to follow the general plan of proceeding from fact to theory.

We shall first take up in detail the study of social behavior of a single species, using this as an illustration of methods of study. With this information as a point of reference we shall compare and contrast the social behavior of other species, which will give us a general picture of the variety of social behavior possible in the animal kingdom. This knowledge provides the basis for the study of social organization and leads us into the field of the development of primary social relationships. Social relationships in turn are the constituents of animal societies, and the special phenomena of territoriality and communication begin to have significance in relation to the organization of these larger groups. Finally, we shall consider animal societies as wholes, together with some of the general theories which explain their existence and operation.

BASIC METHODS OF STUDY

In order to understand fully the social behavior of any animal our first objective is to find out what it can do in a large variety of environmental conditions. This means that the most fruitful studies of social capacities are done with wild species under natural or seminatural conditions, as for example Carpenter's [9, 10] studies of wild howling monkeys and gibbons in their native forests. Domestic animals can often be studied under seminatural conditions. Observing the behavior of captive animals in zoos [29, 30] or laboratories can give us more accurate details, but these environments are so limited that the animals in them show only a small part of their total capacities.

In making such a study on a new animal we begin with what is already known. Social behavior is partially dependent upon the anatomical and physiological capacities of the species concerned, and detailed descriptions of the sense and motor organs are usually available in textbooks of comparative anatomy. However, the basic patterns of social behavior of most species have never been described in detail, and in any case we can learn much by fresh observational study. The following study on the domestic sheep [48] can be taken as a model for others, although the methods used must be modified in accordance with the nature and habits of the particular species concerned [53].

Sheep make a good model for many reasons. Like other domestic animals they can be easily observed in great detail. Their social organization and behavior have not been severely limited by domestication, and under suitable conditions of moderate freedom they develop a social organization quite similar to that of their wild relatives. They show a wide variety of social behavior and social relationships, including most of the important fundamental types. At the same time their social organization is decidedly different from that of primates, so that we are not likely to be influenced by preconceptions and stereotyped thinking derived from human social experience. Finally, their study brings out certain new and exciting facts.

The general method is to observe the social behavior of a naturally formed social group under seminatural conditions. Two pregnant ewes are turned loose together and allowed to live freely in fields with a total area of several acres. Shelter is available in a barn and shed, and in a mild climate it is possible to do without artificial feeding except in short periods in the winter when hay is supplied. The flock is allowed to increase naturally over a period of several years, and we make observations from day to day and season to season.

Motor and Sensory Capacities of the Sheep

We first notice certain facts about their behavioral capacities. Sheep are relatively long-legged animals, capable of fast running for short distances. A related wild species, the Rocky Mountain bighorn sheep, habitually lives in or near rocky cliffs and shows considerable capacities for climbing. Being hoofed animals, they have little power of grasping or manipulating objects, although the hooves can be used to paw the ground or to uncover hidden food. The mouth is never used for lifting or carrying. Sheep prefer to crop grass rather than to browse on twigs and will cut a pasture very short if allowed to overgraze. Like other related grazing animals, the sheep lack upper incisors, and their jaws are of little use in aggressive biting. Many breeds of domestic sheep are hornless, but the skull is quite heavy. Fighting behavior is almost completely confined to butting.

Sheep have some sense of smell and good hearing. However, their dominant sense organ is the eye, as we might expect from the habits of their wild relatives, which are active chiefly in the daylight and rarely go into wooded areas.

A Short Sample of Behavior

We can find many detailed methods for studying social behavior described in another special volume [50]. One of the best and most efficient general methods is to make a number of short observations. These need not be over 10 minutes in length, particularly if the animals are inactive. For example, a flock of sheep may lie down and chew the cud for over an hour without any change in behavior. If, on the other hand, the sheep are unusually active, we can prolong observation.

The knack of observation is one which can be developed by practice. At first we notice only that the sheep are grazing or moving about. After watching them a few times, we begin to see other patterns of behavior. Every now and then a sheep will raise its head from grazing, look around, and then go back to grazing again. If it sees some frightening object, it runs quickly toward the nearest sheep, the others do the same thing, and the result is a compact group which takes off in a direction away from the original disturbance. We eventually conclude that this is a typical pattern of escape behavior.

We find that the best rule for taking notes, either in writing or on a tape or another recording device, is to try to describe everything which the animals do. Theories explaining the behavior will naturally occur to us and we write these down, but always marked in some way to keep them separate from the observed facts. The amount of material which can be accumulated in this way from a daily 10-minute observation over a period of a few weeks is considerable, and it is usually a good idea to try to analyze it while it is still fresh. Since one of our objects is to collect the basic patterns of behavior typical of sheep, the data can first be analyzed by listing each kind of social behavior which we observe. This list is given in Table 9-1.

Table 9-1

Classification of Social Behavior Observed in Sheep *

- *Investigation*
  - Looking at other sheep
  - Touching other sheep with nose
  - Ingestion (nursing)
  - Nudging udder with nose
  - Sucking
  - Wiggling tail
- *Shelter-seeking* (contactual behavior)
  - Huddling together to keep off flies
  - Crowding together in extreme cold weather
- *Agonistic behavior*
  - Shoving with shoulders
  - Running together and butting
  - Running away
- *Allelomimetic behavior*
  - Walking and running together
  - Following one another
  - Grazing together
  - Bedding down together
  - Bouncing stiff-legged past an obstacle together
- *Epimeletic behavior* (in ewes only)
  - Baaing when separated from lamb
  - Walking around and around young lamb
  - Arching back to permit nursing
  - Touching lamb at base of tail with nose
  - Driving dogs away from lamb (stamping foot and rushing with head lowered) †

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* Eliminative behavior has no social significance in sheep. Table reprinted courtesy of Williams and Wilkins.

† Combination with interspecific fighting.

Table 9-1

Classification of Social Behavior Observed in Sheep (*Continued*)

- *Et-epimeletic behavior*
    - Baaing by lamb when separated from mother
    - Baaing by lamb when hungry (bottle lamb only)
    - Baaing by adults separated from flock
- *Sexual behavior* (male)
    - Courtship
        - Hoarse baa or grumble
        - Running tongue in and out
        - Following female
        - Extending neck with upcurled lip, sniffing
        - Nosing genital region of female
        - Rubbing along side of female
        - Biting wool of female
        - Herding or pushing female away from other sheep ‡
    - Copulation
        - Wiggling tail (rare)
        - Mounting female
        - Thrusting movements of hind quarters
- *Sexual behavior* (female)
    - Courtship
        - Rubbing against male
        - Mounting male (rare)
    - Copulation
        - Standing still to receive male

‡ Combination with fighting.

The Daily Round

In watching a flock of sheep we soon see that their activity varies a great deal from time to time and that a fairly regular cycle of behavior tends to be repeated each day. In order to verify this we can make a continuous dawn to dusk study of behavior.

In the early winter season the sheep spend the night in the shed and come out before sunup. After stretching themselves, they begin to graze, spreading out and following a route which leads them into the adjoining field. In the middle of the morning they lie down in the highest part of the field in the sun and chew the cud. All the sheep in the flock form a close group and lie down within a few minutes of each other. As they do so, some of them paw the ground before lying on it. Wild bighorn sheep show the same pattern of behavior as they bed down on the rocky cliffs, where this behavior has the result of producing a small level spot.

An hour or so later they get up, one after another, and begin grazing again. By the middle of the afternoon they work their way around back into the original field and lie down together to chew the cud. There is one more period of grazing before they finally go into the shed and bed down for the night. From this sample we can conclude that the sheep spend most of their time grazing and chewing their cuds, which we may call *ingestive behavior*. In addition, the flock always keeps together as a unit, and all their movements and activities are closely coordinated. This type of behavior appears under the general heading of *allelomimetic behavior* in the table.

A daily cycle in the heat of the summer is quite different. The flock tends to lie in the shed most of the day, avoiding heat and insects. The cycle of grazing and cud chewing is then carried on mostly at night.

The Seasonal Cycle

We discover many more types of behavior when we extend observations over a period of a year. We soon find that the sheep are most active and variable in their behavior at dawn and dusk, and we make as many observations as possible during these times. In late August and September some *sexual behavior* appears. Rams follow the females, sniffing them and attempting to mount. As is characteristic of sheep, the females come into heat for a period averaging about thirty hours. This cycle can be repeated every seventeen days from the middle of September until the middle of March if the female is not bred. If males are present, the females are bred promptly and show only one period of sexual activity. Females show very little sexual behavior, except that of standing still, but the males exhibit a variety of patterns which are listed in the table. It is probable that there is some odor stimulus by the female in heat which excites the male.

During the period of sexual activity males and females stay very close to each other. Several males always gather around the receptive female and attempt to drive each other away by butting from the side or rear. Occasionally there is more serious fighting, in which the two animals draw back a few feet and then rush together head on. Sometimes one sheep avoids the charge of another by dodging or running away. All such behavior having to do with conflict and fighting is called *agonistic behavior*.

The gestation period of a sheep is about five months, so that the lambs are usually born in the early spring. The mothers closely attend their young, anxiously walking around their newborn lambs and going over them inch by inch with nose and lips. They allow the young lambs to nurse and often nose the lambs' tails as this goes on. The young lambs wriggle their tails while nursing. Both mother and offspring appear to be anxious when separated, baaing a great deal and making frantic efforts to get together again.

In these reactions between mother and offspring we can recognize two general types of behavior, *epimeletic behavior*, or the giving of care and attention on the part of the mother, and calling for care and attention by the offspring, which can be termed *et-epimeletic*. Both these types of behavior gradually disappear over a period of months. As the lambs grow older the mothers pay them less and less attention, weaning them completely by the end of the summer. With this information we are able to estimate the relative amounts of different types of behavior occurring in the different seasons, as shown in Figure 9-1.

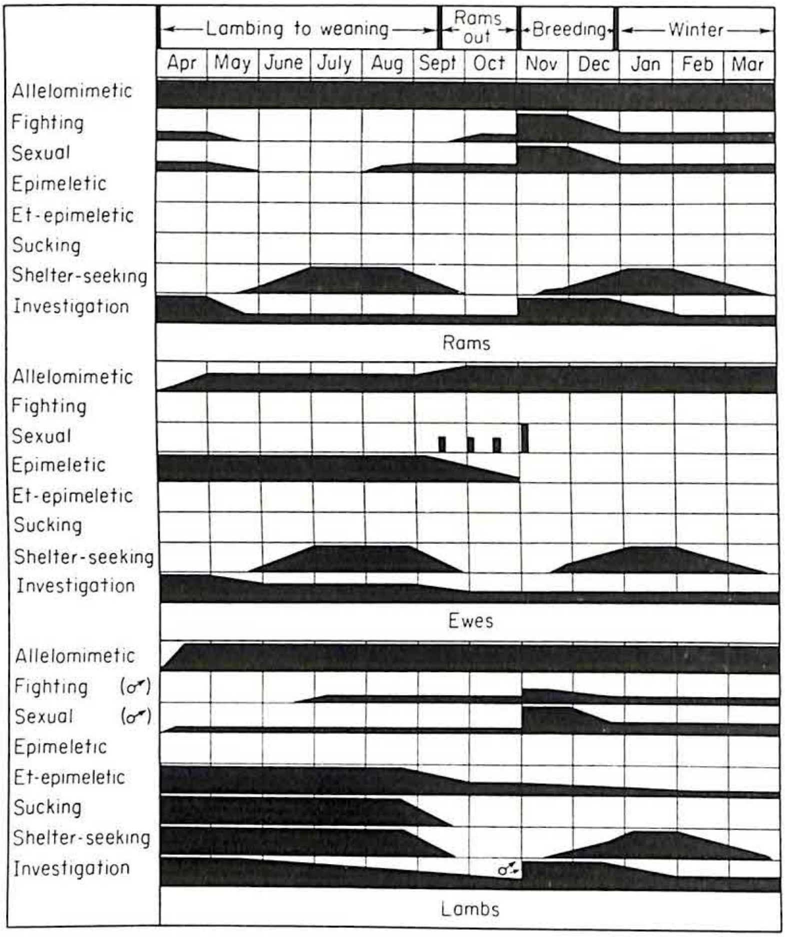

FIG. 9-1. The season cycle of social behavior in a flock of sheep. There are three principal seasons. (*a*) Lambing to weaning in the spring and summer, characterized by the epimeletic behavior of the mothers and et-epimeletic behavior and nursing of lambs. (*b*) The breeding season in the autumn, characterized by sexual behavior and fighting between the males. (*c*) The winter season, in which social behavior is chiefly related to survival and emphasizes ingestive behavior and shelter seeking. Note that the cycle is different for males, females, and young. [*By permission of Williams and Wilkins.*]

Individual Maturation

Still a third way of collecting patterns of behavior is to watch the young lambs as they grow up. When very young, they get most of their nourishment from milk, doing very little grazing before a week or ten days of age. In contrast to the adults they spend a considerable time in playful behavior. When analyzed, this usually turns out to be some form of the adult patterns. Playful butting and fighting is common, and sexual mounting often occurs in the young males. Some other kinds of play have little relation to adult adaptive behavior. A frequent pattern is gamboling, in which the young lambs leap stiff-legged into the air and come down facing in a different direction.

As the lambs grow older we notice that certain definite changes take place. The first of these occurs when the lambs begin to eat grass as well as nurse, which alters the social relationship with the mother. Instead of staying constantly near, the lamb wanders off at a little distance while grazing. A still greater change takes place after two or three months when the lamb is finally weaned and nursing disappears. A third important change is the appearance of complete patterns of sexual behavior at the time of sexual maturity. Along with this the males become more aggressive. A fourth change takes place when the young females begin to bear their lambs and take care of them. Until this time they show no tendency to give any care to others. All of these changes result in a weakening of the social relationship with the mother, so that the growing lamb becomes more independent.

We may conclude that social behavior changes from time to time and from season to season and with the maturation of the individual. These changes are somewhat variable but occur in predictable fashion. The basic method of surveying the social behavior of a species consists of short-sample daily observations of behavior which should be extended over a complete seasonal cycle and from birth to maturity of certain individuals. This data can be supplemented with a few long-sample observations which cover the daily cycle of behavior at different seasons. From all these we can collect the *patterns of social behavior* which are typical of a species and make some estimate of their relative frequency and importance.

COMPARATIVE SOCIAL BEHAVIOR

As shown above, the basic social-behavior patterns of the sheep can be collected under certain general headings. These *types of behavior* may be used as a systematic method for the study and analysis of the social behavior of other species, and they are particularly valuable in comparing

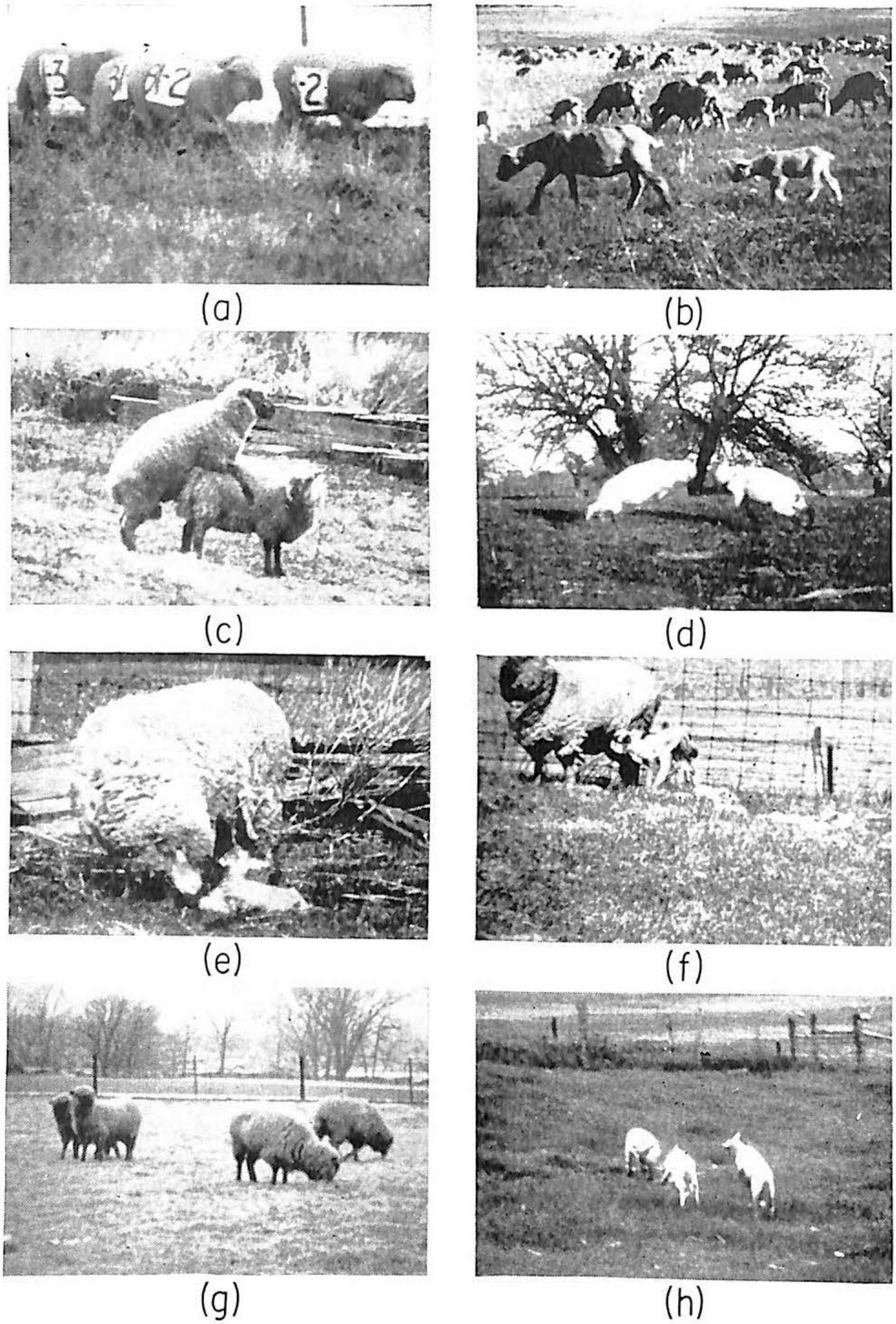

FIG. 9-2. Social behavior of the sheep, illustrated by pictures enlarged from motion picture frames. (*a*) Allelomimetic behavior and leadership in a group of rams. Two males from year 2 are followed by another pair from year 3. (*b*) Allelomimetic be-

and contrasting two species. Certain of these types are primitive methods of adaptation and occur widely throughout the animal kingdom. Others are found almost entirely in highly organized animals. A general list of these types of behavior and their distribution among animals is given below. These are fundamental behavioral activities, and we should become thoroughly familiar with the definitions and use of the terms describing them.

Shelter Seeking and Contactual Behavior. A basic type of adaptation is the ability to move from one environment to a more favorable one. Any animal which can move at all will do this, from Protozoa to primates. As Allee [1, 2] has shown, many, if not all, of these same animals also seek the shelter provided by the bodies of their fellows. Paramecia huddle together on a slide when conditions become unfavorable, and sheep will gather together for warmth. The essence of this behavior is forming contact with the body of another animal, and this *contactual* behavior may be considered a special social variety of shelter seeking. Because of its function, the occurrence of contactual behavior varies a great deal with environmental conditions.

Ingestive Behavior. Special behavior patterns for taking in food are found even in Protozoa like the amoebas, which engulf their food, or in the Infusoria, which drive it into their gullets by the beating of their cilia. Land-living animals may have special behavior patterns for taking in water as well as solid food. Any behavior either of eating or of drinking is called *ingestive*. This type of behavior is therefore almost universal in the animal kingdom, but it has social significance chiefly in those arthropods and vertebrates which feed their young. Worker ants feed both their young and each other. A great many birds feed their young, and in mammals the phenomenon of nursing is universal. Many carnivores like wolves and lions feed their offspring with solid food for a considerable period after weaning.

Sexual Behavior. Sexual reproduction does not imply sexual behavior, since many water-living animals simply release the germ cells into water, where they unite. However, sexual behavior is found in Protozoa like *Paramecium*, which conjugate and exchange micronuclei. In higher animals, it may have very little or a great deal of social significance. In bees, all sex behavior takes place in the nuptial flight, and a queen bee may

havior in a commercial flock of sheep. Note the lamb following the ewe in the foreground. (*c*) Sexual behavior, mounting. (*d*) Agonistic behavior, fighting. The typical behavior pattern in sheep is to run together headlong. (*e*) Epimeletic behavior. A mother stands over her newborn lamb and nibbles the wet fleece. (*f*) Ingestive behavior, nursing. The lamb wiggles its tail as part of this pattern. (*g*) Investigative behavior. The two sheep on the left (a mother and lamb) watch the grazing sheep on the right. (*h*) Playful behavior, gamboling. The lambs run and leap together, a playful form of allelomimetic behavior. [*By permission of Williams and Wilkins.*]

reproduce for months or years thereafter without any further behavior of this type. The usual rule in vertebrates is to confine sexual behavior to a particular season of the year, but social mammals show a great deal of variety. In the sheep, sexual behavior of a female is confined to a brief estrus period which lasts little more than a day. In wolves, sexual behavior of the female may last as long as six weeks. In most primates, sexual behavior is extended over long periods and forms an important part of social organization.

Investigative Behavior. All animals which have the power to move and detect differences in their surroundings tend to explore their environment. Anyone who has studied Paramecia in the laboratory has seen these animals advance, back up, and go ahead in a different direction when they run into an obstacle or changes in the chemical composition of the water. Laboratory rats placed in a new cage go over it inch by inch with the nose and whiskers. Investigatory behavior takes on social significance when individual recognition of other animals is important, as in sexual behavior, fighting, and care of young. That social investigation is important to primates is demonstrated by Butler and Harlow's [6] experiment in which a caged rhesus monkey could open a door to the outside to watch various kinds of objects. Monkeys will learn all sorts of complicated things in order to watch what is going on in the laboratory and are highly motivated by the sight of another monkey.

The above types of behavior are found very generally in all animals which are capable of behavioral adaptation. By contrast, the following types of social behavior are chiefly found in higher animals because of their better developed sense organs and capacities for prehension and manipulation.

Agonistic Behavior (Gr. *agonistikos,* combative). This may be defined as any type of behavioral adjustment having to do with conflict or struggle and may include aggressive and defensive fighting, escape behavior, and passivity or freezing. Escape behavior is found in Protozoa, but aggressive fighting is confined to animals which are able to recognize each other and inflict some sort of damage. There are many cases of social fighting in arthropods, and fighting has been described in all classes of vertebrates.

Epimeletic Behavior (Gr. *epimeleteon,* care-giving). This may be defined as the giving of care or attention. It is frequently given by parents to their offspring and so can be called parental care. However, in the case of many social insects the sterile workers care for the young, and a more general term is preferable. This behavior is highly characteristic of ants, bees, wasps, and termites not only in the care of the young but also in the mutual feeding of adults [71].

The amount of care vertebrates give to their young varies a great deal according to the amount of manipulative skill of the species concerned. Fish at the most do little more than scoop out shallow nests for their eggs and guard them till hatching. Some amphibia also care for the eggs, as for example, those salamanders which lay eggs in a nest and incubate them. Among reptiles, alligators build nests and guard them until after the eggs are hatched. Epimeletic behavior is more highly developed in birds, where both parents often feed and shelter the young, beginning with nest building before the eggs are laid and often continuing until the young birds are almost full-grown. In mammals the amount of epimeletic behavior is quite variable. Some species do little more than nurse their young, while others give them almost continuous attention throughout early life. The limited epimeletic behavior of a sheep with its poor manipulative skill contrasts greatly with the amount of care given by most rodents and primates.

Et-epimeletic Behavior (Gr. *aeteo,* beg, and epimeletic). Among animals which care for their offspring, the young usually call or signal for care and attention. In most cases this calling is a substitute for some adult form of behavior. A young animal may be cold or hungry and make some sort of noise or movement which attracts the attention of the parents. The gaping action of young birds in their nests is an example, as is the baaing of young lambs.

Eliminative Behavior. Many animals, particularly those living in water, have no special patterns of behavior associated with urination and defecation. Elimination becomes a problem in animals which live in nests or lairs [42], and in some species the associated behavior takes on a high degree of social significance. Wolves use eliminative behavior as a way of marking their home ranges, and the same habit is followed by their domestic descendants, the dogs.

Allelomimetic Behavior (Gr. *allelo,* mutual, and *mimetikos,* imitative). This is defined as doing what another animal does with some degree of mutual stimulation. It is found only in animals which have sense organs good enough to keep track of another animal's movements. It is highly developed in schools of fishes, flocks of birds, and herds of mammals. Sheep, of course, have this behavior developed to an unusually high degree. Allelomimetic behavior is seldom found among invertebrate animals, owing to their inferior sense organs. Exceptions are the large-eyed squids, which swim in schools, and the army ants, which move in columns by touching each other's bodies with their antennae.

The Social Behavior of Sheep and Goats: An Illustration of a Comparative Study

We can now summarize the general social characteristics of domestic sheep. Since they constantly keep together in a flock and follow each other's movements very closely, one of the most important types of social behavior is allelomimetic. They spend a great deal of their time in ingestive behavior, but with the exception of nursing, this has little social significance. Though simple in kind, epimeletic behavior by the ewes and et-epimeletic behavior by the lambs is present in large amounts. When the lambs are young, mothers and offspring constantly interact with each other. Sexual behavior is important only in the autumn months, and there is relatively little agonistic behavior. There is no special aspect to eliminative behavior. With their well-developed eyes, sheep are able to investigate each other at a glance. Contactual behavior is common as a protection against cold.

When we compare the behavior of a related wild species such as the Rocky Mountain bighorn sheep, we find many of the detailed patterns of adjustment almost exactly duplicated. The bighorn lambs wiggle their tails when nursing. When the adults are frightened, they rush together in a compact mass and run off just like the domestic sheep. By contrast, they show a great deal more agonistic behavior, both in escape behavior, which is more possible in a wild situation, and in the fighting between males in the breeding season. The wild sheep mature more slowly and do not become sexually mature until the second year. As in most domestic animals, tame sheep apparently have been selected for early maturity, hence greater fertility, and for decreased agonistic behavior, hence easier tameability.

When we do a similar observational study with domestic goats, we find a great deal of similarity in behavior patterns, particularly in the tendency toward allelomimetic behavior. Goats form their own flocks and will readily join those of sheep. However, domestic goats show a great deal more fighting than do sheep. The pattern of fighting behavior is distinctly different. Sheep walk backward, then run together head on from a considerable distance. Goats rear up on the hind feet, turn their heads sidewise and crack them together as they come down. This behavior is correlated with the different shapes of the horns in the two species but is nevertheless seen in hornless individuals of both kinds.

A ram introduced into a flock of vigorously fighting goats was never seen to fight with them. He took his place at the feeding trough and ate while the others fought. Evidently the two species do not respond to each other's patterns of agonistic behavior. Another difference is the presence in goats of a frequent vocal alarm signal which sounds like a sneeze.

The patterns of sexual behavior are quite similar in the two species, and mating will take place, although the embryos never develop to term [68]. One distinct developmental difference is that young lambs follow their mothers from the date of birth, but young kids are left to lie quietly while the mothers graze. The kids may be two weeks old or more before they begin to follow their mothers regularly. Correlated with this is a much weaker social bond between goats than between sheep. We can test this objectively by taking out members of a flock and repeatedly trying to separate them by walking between them. We find that a separation test is effective in goats in 16 per cent of the cases, while sheep only separate in 2 per cent of the cases [61].

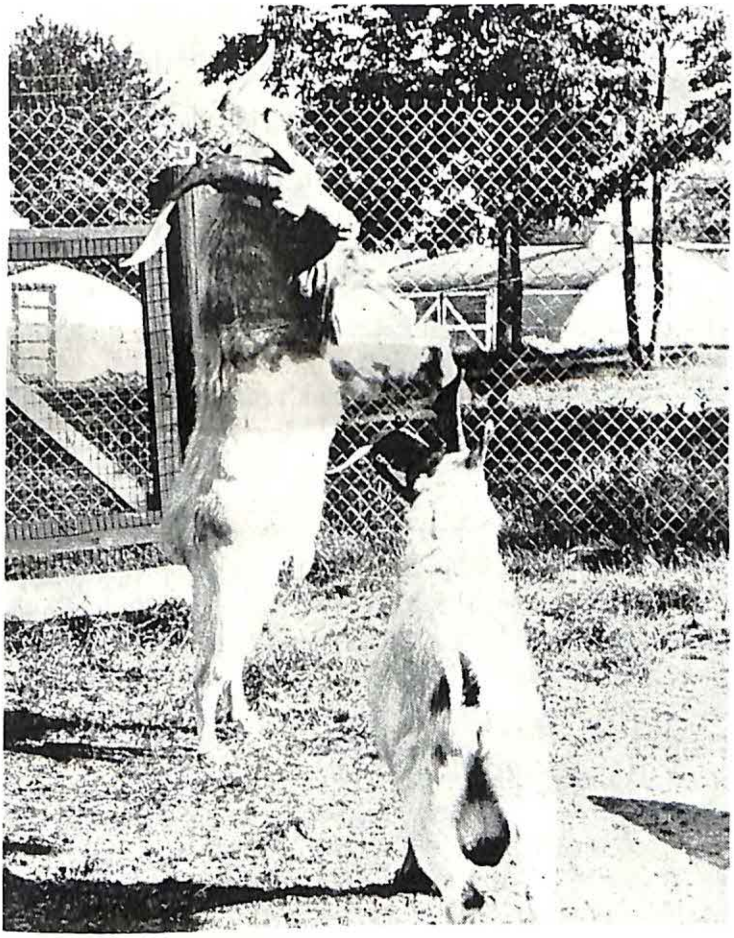

FIG. 9-3. Typical pattern of agonistic behavior in male goats. One or both of the animals rear and butt with a sideward thrust of the head. Compare with the head-on butting of sheep shown in Fig. 9-2(*d*). Animals of the two species apparently will not fight because of the disparity in these patterns of behavior. [*Courtesy of R. Mayo-Smith.*]

This example illustrates a general result of comparative studies: those species which have been classified as being most closely related on the basis of structure are also the most similar in patterns of social behavior.

The two species of sheep, *Ovis aries* and the bighorn, *Ovis canadensis*, are much more alike than either is like the domestic goat, *Capra hircus*. This means that social behavior among these animals is importantly influenced by heredity, which may be either biological or cultural or some combination of the two, as will be seen in the next section.

SOCIAL ORGANIZATION AND SOCIAL RELATIONSHIPS

So far we have considered social behavior chiefly as a response of one animal to a social situation. However, as soon as a group of individuals come together and react to each other, their behavior is no longer independent but has become organized. The behavior of one becomes related to that of others. This concept of relationship is a basic one to social organization, and a *social relationship* may be defined as the behavior of two or more individuals reacting toward each other in a regular and predictable fashion.

Relationships can be described and analyzed on the basis of the kinds of social behavior which are involved. Using the nine different types of social behavior as a basis for analysis, we can calculate forty-five different ways in which these can be combined in a relationship between two individuals each of which exhibits only one type of behavior. The number of combinations is almost infinite if we consider the possibility that the two individuals may each exhibit more than one type of social behavior [51]. Fortunately only a few of these many theoretical relationships are commonly found among animals, and some of the most important ones are described below.

Aggregative Relationships. In a flock of sheep the members often come together and stay in contact without further social behavior. Each individual exhibits contactual behavior. This is a very simple type of social relationship and is found widely in the animal kingdom. As Allee [1] has shown, it occurs in any group of animals which has the power of movement, from Protozoa to vertebrates, and usually has the function of providing mutual protection and shelter.

Sexual Relationships. Both individuals in the pair exhibit sexual behavior. Sexual relationships are widespread among animals and vary from the behavior of temporary breeding swarms of midges and similar insects to the long-lasting mating bonds of some birds and mammals.

Leader-follower Relationships. In this case the behavior of both individuals is allelomimetic, but there is unequal stimulation between the two so that one tends to be slightly more independent than the other and becomes a leader. This type of relationship is highly important in a flock of sheep. Lambs develop the habit of following the mother very early in life and continue the habit into maturity. Adult females still follow their mothers after their own lambs are born. Consequently, in a naturally formed flock there is a tendency for the oldest female to be the leader. There is some tendency among male groups to follow older animals but, since the males never reward the younger sheep by allowing them to nurse, no strong system of leadership develops. Among goats, as might be expected from the fact that the young kids do not follow their mothers from the beginning, there is a much less definite system of leadership. In many other animals the leader-follower relationship is difficult to find or is completely absent.

Dominance-subordination Relationship. In this relationship both individuals exhibit agonistic behavior and, as a result of fighting or force, one individual becomes dominant and the other subordinate. This relationship develops into a strong habit with repetition. In a flock of domestic sheep such relationships are relatively unimportant, and better examples are seen in flocks of hens. Some sort of dominance relationship is found in all animals which show social fighting [12]. It has been described in all classes of vertebrates and many arthropods.

Care-dependency Relationships. In this case the behavior of one individual is epimeletic while the other is typically et-epimeletic. Such a relationship is well illustrated by the behavior of the mother sheep toward her lamb. Whenever the young lamb is cold, hungry, or isolated from the other sheep, it baas its distress call and the mother comes to its aid with epimeletic behavior. Similar relationships are highly developed in the social insects as well as in birds and mammals, and some trace of care-dependency is found in other anthropods and the lower vertebrates. Its development depends in large part upon the possession of enough manipulative skill so that effective care can be given. Among many species of animals a care-dependency relationship is developed with a male parent, as in many birds, or with an animal which is not a parent at all, as in the case of the workers in social insects.

Mutual Care. In this relationship the behavior of both individuals is epimeletic. No good examples are seen in the sheep, but the mutual grooming of monkeys and apes is a good example.

Trophallaxis. This is a complex relationship involving mutual care, which is highly developed in the social insects [71]. When one ant meets another, they first investigate each other with their antennae. Then, if one ant has recently fed, it will regurgitate a drop of honey dew for the other. Investigative as well as epimeletic and ingestive behavior are involved in the relationship.

There are many other possible types of social relationships, some of which are probably never exhibited because they serve little useful function. Others, however, may occur and go unrecognized. For example, among mammals which have definite heat periods there is a regular relationship between males and females which consists of agonistic behavior on the part of the female in response to investigative and sexual behavior on the part of the male.

General and Special Relationships. The usual social group consists of several animals. Each animal has relationships with every other, but not necessarily the same relationships. A young lamb has a tendency to follow any older member of the flock but only nurses from its own mother. The leader-follower relationship is therefore a *general* one, but the care-dependency relationship is a *special* one developed with only one member of the group, the mother.

The Analysis of Social Organization

Each pair of animals in a group may have more than one relationship between them. A male and female sheep may show between them a leader-follower relationship, a sexual relationship, and a dominance relationship, each under different circumstances.

In order to get the complete picture of social organization in a group, the relationships between each pair must be determined by observations or experiment. Since each relationship involves two animals, the total number of relationships in a group of n animals is given by the formula $\frac{n(n-1)}{2}$ [10]. In a group of three there are three relationships; in a group of four, six; in a group of five, ten; etc. The result may also be expressed as an arithmetic series: 0, 1, 3, 6, 10, 15 . . . in which each difference between successive pairs of figures is one greater than the last. It is obvious that a large social group has a very large number of possible social relationships, which makes it hard on the experimenter but not necessarily impossible for the animal. Hens in flocks as large as ninety-six develop dominance relationships in all possible combinations [24], as nearly as can be estimated. Each hen develops 95 relationships, making a total of 4,560 in the flock.

A complete analysis of all sorts of relationships in a group has seldom been attempted. This would involve taking each type of relationship (i.e., dominance-subordination, leader-follower, care-dependency, etc.) and determining its occurrence between each pair of individuals. The total social organization can therefore be extremely complicated. Some experiments speak of a dominance-subordination hierarchy as "the" social order, but it is, of course, only one aspect of social organization. In a flock of goats we find no correlation between leader-follower and dominance-subordination relationships [61].

The organization of a group can be described either from the viewpoint of the group as a whole or from that of one individual. In either case there is a complex network of relationships, with many different relationships between the same pairs. While these relationships may have considerable stability, we should remember that they are constantly forming and developing.

The Forming of Social Relationships

The Biological Differentiation of Social Relationships. As seen in the case of the sheep, the social behavior of the individual varies according to age and sex. This determines the basic organization of an animal group, and its systematic analysis was first worked out by Carpenter in his studies of howling monkeys [9]. Social relationships can be developed between males and females, between females and other females, between males and males, and finally, between each of the two sexes and the young.

There are therefore six possible basic relationships. This fact provides a systematic framework for the description of the social organization of a wild population and its comparison with that of other species. For example, the howling monkeys show strong allelomimetic behavior in all the adult relationships, and the typical group consists of several adult males and females and their offspring. The male-male relationship is unusual among primates in that it includes little or no fighting, which allows adult males to live closely together. The males do not even fight over receptive females, so that there is no division of the group into pairs on the basis of special sexual relationships. The female-young relationship includes chiefly care and dependency, but very little of this is exhibited between the males and young.

By contrast, the gibbons studied under natural conditions by Carpenter [10] show a great deal of fighting both in the male-male and female-female relationships. The typical gibbon group consists of a single adult male, a single adult female, and their offspring. A strong sexual relationship is developed between the adult pair, and care-dependency relationships are developed between both parents and the young.

It may be concluded from this and many other examples that social behavior determines the type of social organization developed in any particular relationship [47]. In the two species of primates above, the differences in social behavior and consequently in social relationships seem to be determined almost entirely by heredity, but training can also be a powerful factor in the determination of a social relationship, as in the following example.

We developed methods for training male mice to fight and not to fight. Animals which had never fought before were taken out, handled roughly, and then replaced in their boxes with a female. After this had been repeated for several days, two males were placed together in the same box. They did not fight at first but lived together for a period of several weeks without fighting and without developing any relationship based on fighting. The next part of the experiment was to teach them to fight. Helpless mice were dangled in front of them and brushed against them. Within a few days they were vigorously attacking the dangled mice. When two individuals which were treated in this way were brought together, they began to fight almost at once and as a result developed a dominance-subordination relationship. The result confirmed the hypothesis that social behavior determines social organization. When no fighting was present, there was no organization based on fighting, but when fighting was present, dominance appeared.

In this last example the difference in social organization was produced by a difference in training rather than by biological factors, and the effect of psychological factors on the development of a social relationship will be discussed in further detail below.

The Psychological Differentiation of Behavior: the Dominance-subordination Relationship. The organization of fighting behavior into a definite social relationship has been thoroughly studied in flocks of hens [24]. When two strange hens meet, they usually begin aggressive behavior after a short period of investigation. A fight follows, with the result that one hen wins and the other runs away. Whenever the two individuals meet thereafter, the hen which won tends to attack while the one which lost stops resisting sooner and sooner. After several encounters, the winning hen has only to threaten the losing one to make it dodge out of the way. The result is a fully developed dominance-subordination relationship.

If a group of several strange hens is thrown together, each pair will go through the same process, so that the new flock becomes organized into a "peck order." In some cases there is a straight-line peck order, with the dominant hen at the top pecking everyone beneath and so on down the line. In other cases the order may not be so clear-cut, with triangles and other relationships possible.

From a psychological point of view the two strange hens present a problem in social adaptation to each other. Each attempts to drive the other away by fighting, but only one can be successful. The hen which wins the fight has its behavior rewarded by success and forms a habit of fighting or attacking. The losing hen is able partially to avoid punishment by remaining passive and avoiding the other, and it forms a habit of escape and nonresistance. Social relationships formed in this way tend to be extremely stable.

Dominance-subordination relationships can be developed both in natural conditions and in the laboratory. In the latter case, artificial competitive situations can stimulate an unusual amount of fighting behavior and develop relationships not seen elsewhere. Goats, which do not compete for natural food, will fight for grain [49]. Captive chimpanzees reared in the laboratory will compete for food, and males will usually dominate females. However, when a female is at the height of sexual receptivity, her male cage mate will allow her to dominate the situation and take the food [74].

The dominance-subordination relationship has been studied in most detail, but other social relationships are presumably built up in the same way. A well-developed social relationship always has certain characteristics: (*a*) there is some sort of mutual stimulation between individuals, (*b*) each individual is able to discriminate between different types of other individuals, and (*c*) the behavior between individuals becomes differentiated either by biological or psychological processes or both.

SOCIALIZATION

Lorenz [36] has described an interesting series of experiments done by the naturalist Heinroth with graylag geese. He hatched their eggs in an incubator and found that the newly hatched goslings would follow the first person whom they saw and that this following reaction was difficult to transfer later to other human beings or to adult geese. In the normal situation the following reaction is, of course, given to the pair of parent birds. Similar experiments with ducks and other species of birds give somewhat similar results, but it is not always easy to get young birds to attach themselves to a human being. Sometimes very specific stimuli, such as imitating the quack of the parent birds, is necessary to elicit the reaction.

In other experiments, Lorenz found that jackdaws, which are members of the crow family and which are hatched in a much more immature state than geese, also have a period in which they can readily form attachments to human beings. He took three birds as naked young and six just before they flew from the nest. Up to a certain time the behavior of all the captives was the same, but as they grew older the birds which had been adopted at a later period became very shy, whereas those taken at the earlier period remained closely attached to him and even gave a mating reaction to his hand. While the period is not so precisely defined as in geese, there is evidently a point in development when it is easy for jackdaws to establish social relationships with another species. Lorenz concluded that the individual to whom social responses are given is not determined by heredity, and he gave this process the name "imprinting."

Comparative studies with mammals and other forms [52] indicate that imprinting is a special example of the process of the formation of primary social relationships which takes place in all social animals. At some time early in development, positive social relationships are built up with a group of familiar individuals. Soon after, other behavioral mechanisms come into play which prevent social relationships being developed with strange animals or with other species. The action of some of these mechanisms may be seen in the following example.

Primary Socialization in the Dog. Puppies are born in an immature state, and their development can be divided into periods based on important changes in social relationships [55]. In the *neonatal period* the puppy is both blind and deaf, and its behavior consists of a few stereotyped patterns of behavior which appear to be reflex in nature. When stimulated by touch, cold, or hunger, the puppy will crawl slowly, throwing the head from side to side, and finally come to rest against any warm, smooth object. Any furry object or even cloth will elicit a sucking reaction. Elimination is produced reflexly by stimulation from the tongue of the mother.

The first obvious change in behavior comes with the opening of the eyes at approximately ten days of age. There follows a *transition period* marked by rapid development in sensory, motor, and psychological capacities and in patterns of social behavior. Hearing appears at three weeks of age, and at this time the puppy also becomes capable of developing avoidance conditioning to any sort of outside stimulus [23]. The puppy first shows reactions of fear, takes solid food, and shows some playful aggressiveness. Studies with the electroencephalograph [11] show almost no brain waves at birth and no differentiation between sleeping and waking states until three weeks of age. Normal adult brain waves are exhibited at approximately seven weeks. The microscopic picture of the early puppy brain shows progressive myelination, or development of the fatty sheaths of the nerve fibers in areas which correspond to the functional changes. All the evidence indicates that there is an important change in the organization of the nervous system at three weeks of age.

The period from three weeks until weaning at seven to ten weeks of age may be called the *period of socialization.* During this time, the first reaction of a puppy to any strange person or animal is one of fear and avoidance, but the puppy cannot travel great distances. If a person maintains contact even for a short time, the fear reactions disappear, and the puppy develops an attachment to and tolerance for that individual. Some puppies will develop an attachment even when their social advances are punished by the handler [21].

Observations on wolf cubs give a very similar result [39]. If a cub is taken before the eyes open, it becomes a tame pet. Wolf cubs display fear reactions to strangers which are similar to those of puppies but much more intense; wild cubs may bite a strange handler severely.

Experiments with puppies raised in large fields apart from human beings show that a pup can be taken out and quickly made into a pet until approximately seven weeks of age, when it may take several days before the puppy recovers from its initial fear. As they grow older, socialization takes a longer and longer time. Puppies taken at twelve weeks of age or older never become completely satisfactory pets and always show more attachment to dogs than to human beings [54].

As with birds, we can conclude that there is a *critical period* in puppy development during which it is easy to establish primary social relationships. In the case of the puppy, contact alone will establish a positive relationship, and this is undoubtedly reinforced by feeding [5]. The negative mechanisms which prevent socialization with other individuals and species are the initial fear and avoidance reactions which, of course, have been considerably reduced in dogs from those which are seen in wolves.

The times at which primary socialization takes place and the behavioral mechanisms involved differ from species to species. In sheep the primary social relationship between mother and lamb is established soon after birth. If the lamb is taken away at birth and returned to the mother as long as 4 hours later, it will not be accepted by her. Up until 4 hours after giving birth the mother sheep will accept any newborn lamb. In this case the critical period is determined by the behavior of the mother rather than the behavior of the offspring [13].

So far, little work has been done on primates, but it is probable that the behavioral mechanisms, though not the times of developmental events, are similar to those in the dog. The "eight-months anxiety" or fear of strangers which is common in human infants [60] probably represents the negative mechanism which prevents socialization to strangers in human beings, and it may be assumed that an important period for socialization occurs before that age.

LOCALITY AND TERRITORIALITY

Locality

In addition to the process of forming primary social attachments, or socialization, young animals show an even more widespread tendency to form attachments to particular physical localities. Except for animals such as jellyfish which are passively carried by water currents, the tendency seems to be almost universal in free-living animals. Limpets, which are tiny mollusks of the seashore, attach themselves to particular spots on the rocks between the tide marks. When the tide is high, they move away a few inches, grazing on the algae, but always return to the same spot. The shell grows so that it fits the contours of this particular rock [44].

Among fish, salmon lay their eggs in the headwaters of rivers. The young fish go back to the ocean, where they grow up, and several years later return as adults to the same rivers where they were hatched. The fish are able to identify the water of a particular river by its chemical composition. In order to get salmon to use a new river system, young fish have to be turned loose in them [27].

Even more remarkable examples are seen in birds which nest in particular localities and return year after year even though they may have migrated thousands of miles in the meantime [37]. The mating spots of the sage grouse of the Western plains are used over and over again for many years and may even continue to be used when a public road is laid through the spot [57]. Similar phenomena are found in many mammals. The white-tailed deer spend most of their lives half a mile or so from where they are born and will not move out of the locality even when the food supply is exhausted. Elk have regular migration routes, going to particular spots in the mountains during the summer and returning to lower altitudes in the winter.

We can therefore conclude that in addition to socialization most young animals undergo an analogous process of *localization* (the word is used here in a sense different from that of sensory localization of an object), in which an attachment is formed to a particular locality.

Localization is, in itself, not a social phenomenon, but it does considerably affect the social life of an animal by determining the individuals with which it comes into contact and therefore can develop a social organization of some kind. It also has an important effect upon the behavior of animals which are artifically moved away from their native environment, and these effects deserve greater study. Its end result is that an animal has a particular home range or locality in which it spends most of its normal life.

Territoriality

In addition to locality, some species of animals show a more highly social phenomenon, the defense of *territory* against members of the same species. That this can be an important phenomenon was first pointed out by Howard in his study of song and territory in bird life [31]. In the English reed bunting, which has habits somewhat like our red-winged blackbird, the males in early spring take command of certain areas in which they sing and from which they drive away all intruders. The territory defended has fairly definite geographical boundaries, and nesting takes place within it. The general effect is to divide up the available breeding territory.

Since Howard's studies were made, territoriality has been firmly established as a common phenomenon in birds [40]. Even colonial species like the cliff swallows [17] have a territory which consists of the nest and the area which the bird can reach from the entrance.

Many mammals definitely do not show territoriality [4]. Most herd animals, like deer, live in certain localities but make no effort to drive strangers out of them. Many nocturnal rodents belonging to the mouse family will attack strange animals when they see them but have no effective way of patrolling particular environmental boundaries, so that the typical picture of home ranges in these animals shows many overlapping edges. Prairie dogs [32] form an exceptional case among rodents. These large ground squirrels are active in the daylight and live in immense colonies. The colony is divided up into definite territories, each of which is usually inhabited by one or two males and several females. If any animal from an adjacent territory crosses the invisible line between them, it is immediately attacked and driven back. When the young in a particular territory have been raised to maturity, the adults move out to the edge of the colony, dig new burrows, and set up a new territory. The result is particularly interesting because it not only protects the young animals but provides for a regular method of colonizing new territories, which is difficult if an animal is rigidly localized. Both locality and territorality have the effect of limiting the movement and social contacts of animals. In addition, territoriality tends to limit population density, which also has an effect on social behavior.

SOCIAL COMMUNICATION

From the earliest times men have speculated on the possibility that other animals have some sort of language, and scientists have quite properly assumed that such phenomena are not likely unless proved by scientific means. However, improved methods and patient work have produced evidence that remarkably complex types of animal communication actually exist. One of the most interesting of these is the system of communication in bees described by Von Frisch [67].

If a bait of honey is put out at some distance from a hive, it will eventually be discovered by a foraging bee, which feeds and returns to the hive soon after. Shortly thereafter a large number of others arrive at the bait, and as they gather food they fly back to the hive in a "beeline." This is the method that the pioneers used to locate a bee tree with its colony of wild bees. It is obvious that the bees have powers of communicating the location of food as well as excellent means of directional orientation.

Von Frisch carefully watched marked bees in a special observation hive as they returned from the baits which he set out. When a foraging bee arrives at the hive, it is at first very active, and the other bees nearby cluster around it. When the bait is close to the hive, the returning bee does a "round dance," running in a small circle, reversing itself, and running back again over the exact same path in the opposite direction. This goes on for as long as half a minute and conveys the information that the food is less than 100 meters from the hive.

If the bait is farther away, the returning bee settles on the honeycomb and does a "wagging dance," which conveys more information. Clinging to the vertical wall of the comb, it runs in a short straight line, wagging its tail. It makes a turn to the left, repeats the wagging movement on the same straight line, turns to the right, and repeats again. The resulting track is a figure 8 with a straight cross bar. The closer the food, the more rapidly the turns are made. The dance also indicates direction with reference to the sun. If the straight run is upward, the food is toward the sun; if downward, the food is away from the sun. Furthermore, if the bee's path is not directly up or down, the angle with the perpendicular gives the angle at which the bee must turn away from the sun in order to find the food. Bees are able to perceive these signals in spite of the almost total darkness within a normal hive, and they can accurately and efficiently locate food at long distances.

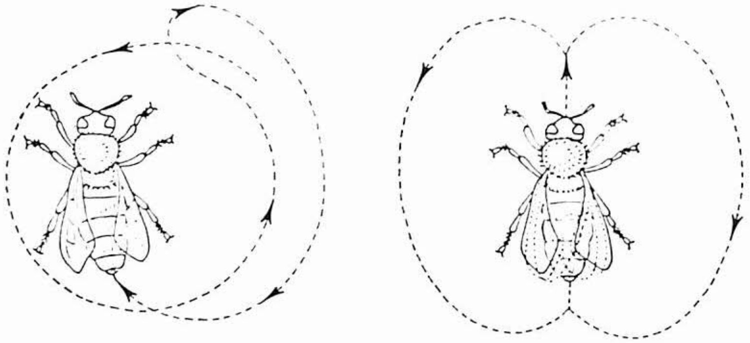

FIG. 9-4. The "round dance" (left) and the "wagging dance" (right). The round dance conveys the information that the food is less than 100 meters from the hive. The wagging dance is done when the food is more than 100 meters away. As the bee makes the straight run it wags its abdomen from side to side. [*From Von Frisch, Bees, their vision, chemical senses, and language. By permission of the Cornell Univer. Press.*]

We may conclude that one bee is able to inform another about the location of a third object. While the information conveyed is quite simple compared to that conveyed by human language and though it is probable that the system of signaling is inherited rather than learned, the bees demonstrate a capacity that has been hitherto unsuspected in animals.

This brings up the possibility that there may be a greater degree of communication in vertebrate animals than is now realized. With modern equipment, vocal signals can be recorded with a great deal of accuracy, even those produced in ranges which are inaudible to the human ear.

When these are played back, the responses of the animals give an experimental test for communication. Frings [22] has shown that playing a recording of the distress call of starlings will cause flocks to leave an area. Work of this sort is still in its infancy, but it does look as if some of the responses of birds to vocal signals are in part learned and that the effects will wear off if signals are simply repeated without any reward or reinforcement. Earlier workers [63] have shown that the songs of some species are learned from the parents, although this is obviously not the case in cuckoos, whose eggs develop in the nests of other species.

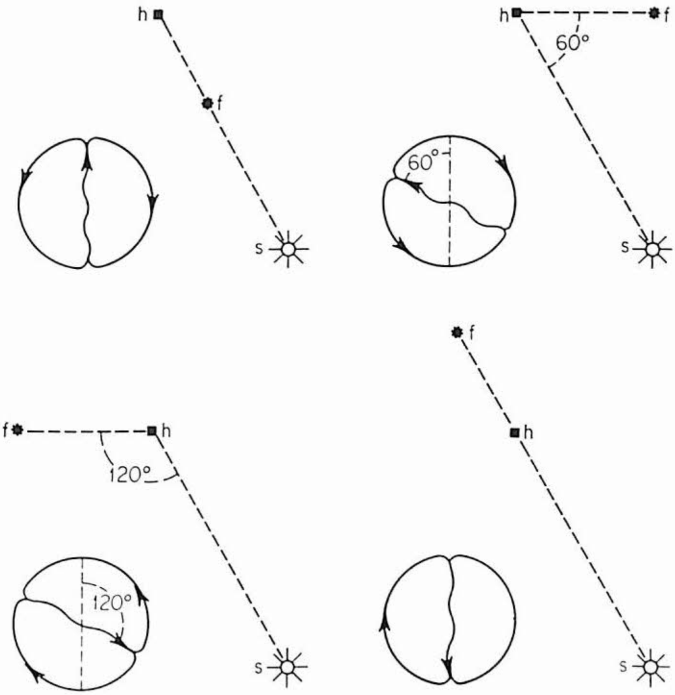

FIG. 9-5. Showing how the wagging dance indicates the direction of the food. Going straight up means that food is toward the sun; straight down means away from the sun. The angle from the vertical, and whether it is to the right or left, indicates the position of the food in relation to the sun. [*From Von Frisch, Bees, their vision, chemical sense, and language. By permission of the Cornell Univer. Press.*]

Many birds have excellent capacities for imitating and repeating sounds [38]. Mammals in general are poor in this ability, although many of them make high-frequency sounds which have never been thoroughly studied from the viewpoint of communication. Most experimenters have centered their efforts around the problem of training mammals to learn human speech. The results are meager compared to those with talking birds. Various experiments with chimpanzees reared like children in a human family have produced only one or two words learned with great difficulty [28].

Like dogs, cats, and other domestic mammals, chimpanzees can learn to respond to human speech. For the most part, words and phrases are associated with particular responses, in the same way that animals learn to respond to whistles and buzzers in conditioning experiments. There is little evidence that animals can understand words when used in new combinations to convey different commands from those expressed before, and much evidence that trained dogs depend a great deal on visual signals as well as spoken commands. However, learning to respond to signals could result in a considerable amount of simple communication between animals themselves under natural conditions. Chimpanzees have a considerable variety of sounds which they make toward each other [41]. How much information this could convey between chimpanzees raised in natural social groups is not yet known.

The whole area of animal communication is one in which rapid advances are being made at the present time, and the results have considerable bearing on the problem of social integration.

THE COMPARATIVE STUDY OF ANIMAL SOCIETIES

An animal society may be defined as a group of individuals whose behavior is organized into social relationships. The type of society depends upon the kinds of social relationships which receive the most emphasis and these, in turn, depend upon a great many other factors, such as the biological division of labor in the species, the sensory ability to discriminate between different individuals, the psychological capacity to form relationships based on learning, and finally, the motor ability to enter into certain kinds of relationships, particularly those involving the care of offspring. As indicated in previous paragraphs, the types of social relationships developed also depend upon the types of social behavior present in the species.

Aggregations

The vast majority of lower invertebrates have no lasting social groups but frequently come together in temporary aggregations. Most of these groups are based on contactual behavior which protects the animals from unfavorable conditions. Other temporary aggregations may be based on sexual behavior. In spite of the brief duration and low degree of organization of these groups, they are important in that they probably once provided the basis for evolution of higher degrees of organization [2]. Social groups having the function of reproduction developed into groups having highly elaborate social relationships involving the care of the young.

Prolonging the period of contact between members of a group provides the basis for the evolution of allelomimetic behavior and the elaborate organization of flocks and herds of higher animals.

Insect Societies

Some degree of social organization is present in many arthropods, but its highest development among invertebrates is seen in insects, whose societies are primarily characterized by great emphasis on care-dependency and mutual-care relationships. The most elaborately organized insect societies occur in the orders Isoptera (termites) and Hymenoptera (ants, bees, and wasps).

The ant may be used as an example [71]. At the time of the nuptial flight, male and female pairs mate, discard their wings, and dig a small nest. From this time on, the male-female relationship is unimportant. The female can produce two kinds of eggs: fertilized eggs which develop into females and unfertilized eggs which develop into males. The males are produced only at the swarming season. The females are divided into two classes: sterile females, or workers, which establish care-dependency relationships with the developing young, and fertile females, or queens, which are produced only at the time of swarming. The worker females show the complex relationship of trophallaxis. All of these relationships seem to be primarily determined by biological means, either heredity or special-feeding. However, psychological differentiation is not completely absent, as is shown by the slave-raiding ants. These ants have no workers but steal the young from other species. Developing in the strange nest, the slaves become socialized to their captors, will take care of their offspring, and will drive off members of their own species.

Other types of insects develop more complex social organizations [2], with greater differentiation on either a biological or psychological basis. Termites may have several different biologically determined classes of individuals, including soldiers as well as workers and each having a different behavioral function in the nest. In honey-bee hives the worker females do different sorts of tasks in a regular progression as they grow older. However, the insect type of social organization is very different from that in vertebrates, both in the more elaborate biological determination of social relationships and in the greater emphasis on care-dependency relationships at the expense of all others. Furthermore, there is at present no good evidence that either leader-follower or dominance-subordination relationships are important in insect societies.

Vertebrate Societies

There is a great deal of variety in the societies of vertebrates, but all of them show the basic biological differentiation in the behavior of males, females, and young. Among many species of fish, allelomimetic behavior is highly developed and results in the formation of schools. The relationships between different fish in a school are little differentiated, and there is no indication of a leader-follower relationship. A school of fish is very similar to the social group developed by squids, which are marine mollusks and entirely unrelated to fish but which also swim and show allelomimetic behavior. Another social relationship characteristic of many fish is that between the male and young. Courtship and sexual behavior of a species like the stickleback last but a short time. After this the male remains and guards the nest until the young hatch [64]. In this and some other species like the river dogfish [16], the young fish stay with the male for a short period and are guarded by him. The care-dependency relationship in fish is never highly developed, probably because of the poor manipulative abilities of these animals.

Little is known about social organization in Amphibia. Since many of them are both nocturnal and aquatic, they are difficult to study. Test [62] has described the behavior of a South American form which shows a defense of territory and probably develops dominance organization. The social organization of most reptiles has likewise been little studied. Snakes tend to form aggregations during cold winter weather. Lizards show dominance and territoriality, and alligators guard their nests and develop at least some care-dependency relationships [19]. The Galapagos tortoises will develop a dominance order when kept in a zoo [20].

A great variety of social organization is found in birds. Like the insect societies, there is a strong emphasis on the care-dependency relationship. Unlike the insects, however, we find that birds of both sexes often take part in the care of the young. In a typical society of perching birds, sexual relationships may last over a period of several weeks and throughout the breeding season, and the same individuals may mate again, year after year. The dominance relationships are important in relation to territory, the resident bird usually being dominant as long as he stays on his home ground. Outside the breeding season, allelomimetic behavior is very important, resulting in the formation of flocks of hundreds and even thousands of individuals.

In many species, flocks show no high degree of differentiation of behavior, but definite leader-follower relationships are found in ducks and geese. There is a strong tendency in most birds to change the type of social organization with the season of the year. During the breeding season, sexual, care-dependency, and dominance relationships are very important. During the rest of the year these may disappear almost completely, being replaced by a simple allelomimetic relationship in the flocks.

A similar variety of social organization is found among mammals, many of which show seasonal changes in social organization, like the birds. Rodents emphasize the care-dependency relationship, and a great deal of their social contact takes place within nests. Dominance organization is usually well developed, but, as indicated above, few species show defense of territory. Aggregations are common in the winter season. The most highly developed rodent societies are found in the ground squirrels, which also show a considerable degree of vocal communication. Rats [7] raised under seminatural conditions develop a moderately high degree of organization, emphasizing the care-dependency and dominance relationships.

Sheep have a social organization which is typical of many herd animals. The most important social relationship is that between the mother and offspring which, of course, has a biological basis. The care-dependency relationship is important, and as a result of this the pair develops a strong leader-follower relationship. No special relationship is developed between adult males and young. The next most important relationship is that developed between young and other young born in the same season, as this also tends to be maintained in adult life. The young-young relationship is largely allelomimetic to begin with, but a mild dominance-subordination relationship may be developed as the animals grow older. There is a tendency for adult males to form separate groups from the females, and mild sexual relationships are sometimes developed in the male groups.

All of the above relationships are specific ones in which only special individuals are involved. In addition, certain general types of relationships are developed. The young lambs tend to follow any older sheep, even a stranger. The females develop a dominance-subordination relationship with all lambs which are not their own, and the lambs soon learn not to try to nurse females which are not their mothers.

The relationships between the adult males and females is very weak, as sexual behavior is of brief duration. There is nothing corresponding to the primate family organization of male, female, and offspring.

In general, ruminant animals typically form herds of varying sizes, and there is a great development of social organization based on allelomimetic behavior. In some herds such as the red deer [15], leader-follower relationships are highly developed. There is some emphasis on the care-dependency relationship between the females and young, but sexual relationships are of little importance except in the brief breeding season. Dominance organization is important within a herd. These relationships always appear to be individual, and no case of group attacks on an individual has been so far discovered. On the other hand, a mutual defensive relationship is common, and is probably most highly developed in musk oxen.

Those carnivores whose societies have been studied show tendencies toward prolonged sexual relationships, and mating is frequently reported to take place for life. In foxes raised by breeders, it is extremely difficult to get the males to mate with more than one female [18]. There is also much greater emphasis on the care-dependency relationship, and many carnivores feed their young for long periods. Capturing prey is a difficult process for a young animal and in many species, particularly in the cat family, the young seem to learn this from their parents. In any case, there is a long period of dependency. Some carnivores, like wolves [39], show much allelomimetic behavior and organization into a pack. The origin of the pack appears to be a litter of several individuals. There is no highly differentiated organization or clear leadership, but members of the group often combine activities, both for attacking prey and defense against larger predators such as bears. Dominance relationships are highly developed and seem to be particularly important during feeding.

Most primate societies emphasize the sexual relationship, with prolonged sexual activity and a tendency in some species to form semipermanent relations between mates. Care-dependency relationships are also highly developed, chiefly involving the female and young but occasionally, males also. Mutual care is frequently seen. Primates such as baboons [75] and rhesus monkeys form large hordes, combining typical family groups of males, females, and young. Within such groups there seem to be some leader-follower relationships. In howling monkeys the males usually lead the females, but there is no one leader of the group [9]. Dominance organization varies with the degree of agonistic behavior and is strongly correlated with sexual relationships. However, adult males of some species may combine in group attacks against predators. Like other mammalian groups, the primate societies vary greatly from species to species.

We can conclude that a variety of social organization is possible *within* the same broad taxonomic group. Various factors seem to account for this, but particularly the types and amount of social behavior which are determined by the heredity of the species. Equally great variation in social organization is found *between* broad taxonomic groups. In addition to heredity, the general ecology (environmental relationships) of a class of animals has strong effects on social organization. The herd mammals typically live under plains conditions and eat vegetable food. There is usually little competition over food, and little skill is required in getting it, so that neither dominance nor care-dependency relationships are highly developed, although domestic herds readily develop dominance relations around the feeding trough. The chief problem of these animals is dealing with carnivores, and their highest degree of social organization is centered around escape.

On the other hand, carnivorous mammals depend on a food supply which is widely scattered and often difficult to get. They are rarely found in large numbers, and these are kept down by a strong territorial system. The nature of their food requires a long period of dependency and learning on the part of the offspring.

Finally, most primates are arboreal, which creates a special problem of care of the offspring, which are likely to fall out of the trees unless carried and helped. In most species the young are carried for at least a couple of years, when their motor development has proceeded far enough so that they can move on their own. This produces a prolonged period of dependency. Some primates are both carnivorous and herbivorous, and they may show tendencies toward group action in both offensive and defensive fighting. In general, primates show greater social differentiation and variety of social relationships than do other mammals and, hence, develop more complex social organizations.

EXPERIMENTAL STUDY OF SOCIAL BEHAVIOR AND SOCIAL ORGANIZATION

Both descriptive and experimental studies have contributed to the general principles of comparative social psychology stated above. Experimental studies in social psychology are essentially different from those in which the social factor is unimportant. By definition, social behavior involves more than one individual, and in most experiments the basic variable is not that of an individual but of the relationship between two or more individuals. This creates many special problems of procedure.

There are two major groups of experimental problems in social behavior. One of these concerns the *effects* of social behavior upon social organizations, and on a higher level upon the organization of populations. This type of research has already been illustrated in the studies of peck orders, the processes of socialization, and the phenomena of locality and territoriality. The second concerns the *causes* of social behavior, which may be hereditary, physiological, environmental, and even include the process of learning. One basic problem is whether the general "principles of learning," which have been so largely developed from experiments with ingestive behavior, will apply to other forms of social behavior as well. A second concerns the ways in which hereditary factors produce their effects on social behavior. Another consists of tracing the complex network of physiological causes which affect each type of behavior.

Still another group of experimental studies has been concerned with the problems of social motivation. Animals which show allelomimetic behavior, such as monkeys [26], puppies [43], fish [70], and chickens [3], will eat more in the presence of others than when they are fed alone, even when there is no competition. Laboratory rats, which show little or no allelomimetic behavior, eat increased amounts of food if there is competition but not otherwise [25].

Similar results are obtained in other situations where there is a food reward. Dogs [66], which are strongly allelomimetic, run faster through alleys when in familiar pairs than when alone, while rats [33] do not. Again, in solving mazes, groups do better than individuals in the allelomimetic fishes [70] but not in rats [69].

It is obvious that the mutual stimulation which is part of allelomimetic behavior has an important effect on the motivation of animals which behave in groups. This effect, which has been called *social facilitation*, in part depends upon the hereditary constitution of the species tested.

Competition is another aspect of social interaction whose effects can be tested experimentally. As stated above, rats will eat more food if there is competition, but if pairs of rats are run through an alley and only the winner gets the food, the losers soon run more slowly and the winners run no faster than when alone [34]. Cats [72] react in the same way, and we can conclude that strict competition has an effect on behavior which can be deduced from the laws of learning, namely, that behavior which is not rewarded because of competition tends to disappear or be extinguished.

HISTORY OF THE STUDY OF SOCIAL BEHAVIOR

The modern science of animal behavior begins with Darwin. His theory of natural selection of individuals who had highly adaptive behavior tended to concentrate attention on the individual, and for many years most scientists assumed that there were only two kinds of social animals, the social insects and man. The social behavior and highly integrated societies of insects could not be disregarded, and many excellent studies were done upon them, culminating in the discovery of trophallaxis as the basic social relationship in many insect societies.

Meanwhile, studies of social behavior in other animals were largely anecdotal in nature. Many excellent observations were made in connection with other types of research, and some of the early literature contains fascinating information. However, the interpretations are often biased from the viewpoint of the particular social culture of the author and sprinkled with such arguments as monogamy versus polygamy and democracy versus autocracy [58].

A new era in comparative social psychology began after the First World War, with a mounting appreciation of the extensive social behavior of birds. Howard's study, *Territory in Bird Life* [31], demonstrated the existence of complicated social organization among these animals. Other experimenters have since extended his findings to most of the perching birds and in modified form into many others. Meanwhile the Norwegian

Schjelderup-Ebbe [45] identified the individual members of a flock of domestic chickens and discovered that they were organized in a stable peck order. Since that time instances of social dominance and subordination have been found in all classes of vertebrates and in many arthropods [12]. This relationship can be of great importance in natural populations [56] and is more than an accidental result of domestication.

Lorenz [36] studied the development of social relationships in birds and found that the primary social attachment of a young bird often took place within a few hours after hatching and that this social relationship could be in some cases transferred to other birds or even human beings. Tinbergen [64, 65] and other ethologists became interested in studying the instinctive or hereditary nature of basic social-behavior patterns, and much of their work has wider implications.

In the same era, Allee [1, 2] became interested in the simplest sort of social organization, the temporary groups of animals which are formed by almost all members of the animal kingdom under unfavorable conditions. He showed that these groups yielded definite physiological benefits to their members and that this primitive type of social behavior may have been the basis for the evolution of more complicated social organization. At the other extreme of social complexity, Carpenter's [9, 10] field studies of primates laid down a scheme for the study of basic social relationships in animals.

Most of the above work was done by biologists, while psychologists became interested in the phenomenon of social facilitation [14, 59]. This important problem of the sources of social motivation has since been partially lost to view amid the theoretical controversies involving learning theories which explain the behavioral reactions of solitary animals to feeding and electric shock.

Meanwhile, many new advances have been made in the behavior of social insects, particularly in termites [2], army ants [46], and the "language" of bees [67]. The study of the social behavior of mammals is now coming to the forefront of research, particularly in relation to the social organization of populations [8] and the effects of early social experience [52].

SUMMARY

There is still a dearth of factual material regarding the social behavior of animals. In this short chapter we have surveyed basic methods of study, the kinds of phenomena which occur in social behavior, and the general principles which explain them. Both facts and principles need to be studied in many other species.

The primary method of investigating social behavior and organization is observational, used preferably in a natural environment and in a naturally formed group of animals. Only in this way can the full expression of social capabilities be observed. An essential part of observation is recognition of individuals and, since behavior varies with environmental and internal changes, observations should cover both the daily and seasonal cycles and the development of behavior. Once the basic facts have been obtained in this way, experimental studies can follow, and one of the basic experimental methods is the measurement of the reaction of pairs of individuals to each other in various situations.

Observation reveals various sorts of social phenomena. There are among animals nine important types of behavioral adaptation, each of which may have at least some social significance. Each species has characteristic *patterns of social behavior* through which it meets these problems of adaptation, and these can be used as a systematic method of describing the social life of a species and comparing it with others. A second phenomenon is the *social relationship,* the tendency for animals to exhibit regular and predictable behavior toward each other. These relationships result from the organization of the basic patterns of social behavior. Each species has a limited number of important relationships; often only one or two of them are emphasized. A third phenomenon is that of *socialization.* Every social species has certain behavioral mechanisms whereby, early in life, an individual forms attachments with a few members of its own species and is normally prevented from forming such attachments with strange individuals and members of other species. The behavioral mechanisms differ from species to species, and some are much more flexible than others. Finally, most animals show an analogous phenomenon, that of *localization.* Early in life many animals tend to become attached to particular localities and, under special conditions which usually include the sensory ability to recognize a boundary and the ability to fight, these localities may be defended as *territories.*

These phenomena may be explained and defined by several important general principles. One of these is that the essential differences among animal societies are based on hereditary differences in form and function which limit the kinds of behavior and social organization that are likely to be manifested by the species. This is the genetic basis of social behavior. On the other hand, social behavior is also affected by the kind of environmental situation in which the group of animals is placed and to which they must adapt. This is the ecological basis of social behavior. Finally, their behavior is modified by previous experiences through the process of learning, and this is the psychological basis of social behavior.

The formation of a social relationship is a process of differentiation involving biological growth on the one hand and the psychological phenomenon of learning on the other. One of the principal determinants of a relationship is the type of social behavior which the animals exhibit toward each other, and another is the process of learning in which the two individuals adjust to each other's behavior. Some species may have social relationships determined almost entirely by biological factors, but in the higher animals the factor of learning is always an important one. In general, the degree of social organization depends on the degree of differentiation of behavior produced by the combined action of biological and psychological factors.

Each animal society has some characteristic process of socialization whereby primary social relationships are determined. In most societies this takes place in a limited period early in life, which may be described as a *critical period* for the formation of social relationships. What happens in this period determines the individuals to which an animal becomes related and, under experimental conditions, even determines the species with which these relationships are formed.

With all these factors affecting the behavior of individuals, it follows that their behavior can be completely understood only in terms of the animal societies to which they belong. An experiment on animal behavior is not performed in a social vacuum. Even when an animal is completely isolated, its very isolation may contribute to its behavior. In this way many of the hitherto mysterious aspects of animal behavior are now becoming understood.

The study of comparative social behavior involves all of the phenomena ordinarily analyzed in psychology: the factors of heredity, sensory abilities, learning, motivation, etc., which have been described in other chapters of this book. Hereditary factors determine an animal's capability for social behavior, and social relationships may be differentiated through learning. Each of the different types of social behavior presents problems in the origin of motivation. In addition, the fact of social organization results in certain new phenomena, such as social relationships, which in turn affect the behavior of individuals. The phenomenon of socialization affects the behavior of most experimental animals used in the laboratory, and it is obvious that the quality of the social relationships formed during the critical period has an important bearing on the problem of abnormal behavior, which is the subject of the next chapter.

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CHAPTER 10

Studies of Abnormal Behavior in Animals

> I am convinced that the decision . . . of many important questions of etiology, the natural systematisation, the mechanism and finally the treatment of neuroses in the human being lies in the hands of the animal experimenter.[*]

Abnormal behavior in human beings is ordinarily studied in clinical or hospital settings as part of a program designed to alleviate the patient's difficulties in dealing with himself and the world about him. But, as a by-product rather than the main objective of clinical practice, this type of research faces severe restrictions. For the clinical investigator is limited in his operations by the precious nature of the human material with which he is working; he is not free, as other investigators are, to manipulate possible causal influences in a completely arbitrary manner simply to see what effects they may have on the behavior he is investigating; he is ethically constrained not only to avoid measures that might be damaging to his patient but, positively, to seek out and use the most effective techniques that he can find, in the present state of his knowledge, to promote a favorable outcome in the individual case. Consequently, clinically based theories have long suffered from a surplus of speculation and a shortage of systematic data.

Use of Animal Subjects

In other fields where the original material is too valuable to be used for the sole purpose of gathering information, scientists and engineers have often turned to laboratory models or replicas of the systems they wished to study. The civil engineer, for example, may build a scale model of his bridge or dam in order to find out where the weak spots are and what strains and stresses the structure will bear. The medical scientist may use other species in order to study the progress of a disease, determine the effects of surgical intervention, or test the action of a new drug or serum. Similarly, the behavioral scientist or engineer may turn to the laboratory to reproduce the "field of forces" he has observed in a natural or "real-life" setting. From such a working model he hopes to determine what is contributed to the behavioral outcome by each of the relevant environmental happenings. For this purpose, animal subjects are expendable. A considerable degree of control can be brought to bear on their individual heredities, their personal histories, and their current circumstances, even to the point of exposing them to conditions that are clearly not to their best interests as individual beings. Furthermore, the basic laws by which they function may be laid bare, with no overlay or distortion by behavior learned to meet the special requirements of a given human culture. "From the study of such a skeletal psychological environment," declares one investigator, "it will be possible to identify the traumatic factors responsible both for animal and human neurotic behavior" [34, p. 579].

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[*] Ivan P. Pavlov, *Lectures on conditioned reflexes.* Vol. 2. *Conditioned reflexes and psychiatry.* (Trans. and ed. by W. H. Gantt.) New York: International Univer. Press, 1941. P. 74.

Two Types of Research

In this chapter, then, we shall consider two main types of work. First we shall take up studies of what has been called "experimental neurosis," using a term first suggested by Pavlov. This type of work has largely been conducted by medically oriented investigators—physiologists and psychiatrists—who tend to think of a neurosis as a single underlying entity, like a disease, which expresses itself through a standard set of "symptoms." Their aim is first to "make the animal neurotic" by exposing him to some form of stress or conflict and then to describe, often in rather subjective and qualitative terms, the resulting changes in his behavior. Various means of treating the neurosis are often tested, but little attempt is ordinarily made to ferret out more specific relationships between what has been done to the subject and each of the individual changes that has taken place in his behavior.

Later in the chapter we shall consider some of the studies in which the experimenter has concentrated on a single relationship and has attempted to specify both his procedure and his outcome with greater precision. But to avoid surveying the entire body of research directed toward the discovery of general laws of behavior (behavior theory), we shall limit ourselves to those studies that have grown directly out of clinical theories or that seem most immediately relevant to clinical observations. Also, to give adequate attention to relatively general processes we shall pass over such highly specific procedures as brain surgery, high-frequency auditory stimulation, electroconvulsive shock, or the use of pharmaceutical agents, which are defined in terms of their physical rather than their functional characteristics.

EXPERIMENTAL NEUROSIS

Studies from Pavlov's Laboratory

In all likelihood, the first experimenter to make use of animal subjects to study the development of abnormal or pathological behavior was Pavlov, the famous Russian physiologist. Pavlov, you will recall, is better known for his early work on the functioning of the digestive glands, which won him the Nobel Prize for medicine in 1904, and for his subsequent studies of the way in which new stimulus-response connections are established. But just as his early studies of innately determined or "unconditional" digestive secretions led him to investigate the strange power of associated sights, sounds, and odors to evoke "conditional" secretions of the salivary glands, so the conditioning studies of his middle years, which he viewed as studies of "the higher nervous centers" (brain), led him to study disorders of functioning both in the laboratory dog and in the human patient.

First Observations. Pavlov's attention was first called to the problem of neurotic behavior by the work of one of his students, Yerofeyeva, in 1911. Electric shock was being used as the conditional stimulus for salivation. A weak current was used at first, coupled with the meat powder which was the unconditional stimulus for the salivary response. Gradually the strength of the current was increased, step by step; continued application of the meat powder maintained the salivary response and suppressed the normal "defence reaction" (struggle and attempts to escape). After the response was securely established to a "very powerful" stimulus, Yerofeyeva began a new line of investigation; now she applied the electrode to other areas of the skin surface in an effort to extend the spatial locus of the reflex. "A limit, however, was suddenly reached. When a still further place was added to those already successfully generalized everything underwent an abrupt and complete change. No trace of the alimentary [salivary] reaction was left: instead only a most violent defence reaction was present" [56, p. 290].

At first Pavlov thought that Yerofeyeva's finding might be a special result of using shock as the conditional stimulus. But in 1914 he observed a similar disturbance in a study by Shenger-Krestovnikova. This experimenter had been training his animal to discriminate between a perfectly round circle of light projected on a screen in front of him and a similar patch of light in the shape of an oval or ellipse. The dog was expected to salivate when the circle was presented, since this was followed by food, but to refrain from salivating when the ellipse was presented, since this was not followed by food. In the early stages of the experiment the discrimination was easy, since the ellipse was only half as broad as it was long and did not look very much like a circle. As the experiment continued, however, Shenger-Krestovnikova gradually increased the width of his ellipse until it was almost as wide as it was long, that is, almost circular. At this point the dog could no longer distinguish between the two stimuli. His discrimination gradually deteriorated, and he became excited and unruly, calming down only when the discrimination was reestablished at an easier level. "After these experiments," wrote Pavlov, "we paid considerable attention to pathological disturbances in the cortical activity and began to study them in detail" [56, p. 292].

In 1918 Pavlov spent his summer months at a mental hospital collecting first-hand observations of human patients to compare with the behavior of his dogs. During the following decade he devoted more and more attention to this problem, conducting additional experimental studies and further developing his theories of the relationship between the human manifestations and those of the dog. During the last few years of his life, from 1930 to 1936, he spent most of his working time at this task. On a visit in 1933, Gantt reports, "Several times a week he visited psychiatric wards and discussed cases with the psychiatrists . . . His desk was covered with the current texts of psychiatry in English, German, and French" [57, p. 12].

Procedures Leading to Neurosis. A number of procedures have been used at one time or another in Pavlov's laboratory to produce "experimental neuroses," as he called them. These procedures have been summarized by one of his students, Ivanov-Smolensky, as "the administration of ultra-powerful stimuli . . . ; the elaboration of excessively delicate or numerous differentiations [discriminations] . . . ; a considerable prolongation of a differential stimulus . . . ; the elaboration of difficult differentiations between complex, synthetic stimuli . . . ; the elaboration of a conditioned response to every fourth successive stimulus . . . ; a quick, direct transition from an inhibitive stimulus to a positive one . . . ; and finally . . . an abrupt change of the accustomed order . . . in the system of positive and inhibitory conditioned reflexes, which had been repeated and trained from day to day under one and the same stereotype [sic] sequence of stimuli and intervals between them" [24, pp. 113 and 114]. Pavlov himself believed that all of these techniques involved the "overstraining" or "collision" of certain hypothetical neural processes, but it is obvious that the essential conditions for the production of these disturbances have never been fully isolated.

Two Types of Reaction. The effects of these training procedures take two forms, according to Pavlov, depending on the native constitution of the dog that is used as the subject. In the more "excitable" type of dog, responding occurs when it is not wholly appropriate; the dog salivates to the inhibitory as well as the positive stimulus, responds prematurely when a long interval is employed between the conditional and unconditional stimuli, and is slow to extinguish when the unconditional stimulus is omitted from the picture. This type of animal shows some signs of restlessness and agitation whenever a new inhibition is attempted and may become unruly when the discrimination becomes too difficult to master. Pavlov related this type of reaction to the manic-depressive psychosis in human patients.

In the "weak" type of dog, on the other hand, the response may dwindle or disappear when the discrimination becomes difficult, and the animal becomes unusually quiet in his general deportment. Pavlov related this reaction to schizophrenia and special cases to psychasthenia, neurasthenia, hysteria, and such symptoms as compulsion, phobias, and melancholy [18, p. 233; 57, p. 163].

Comment. The resemblance of these patterns of behavior to those observed in human neuroses seems casual, at best, and it is difficult to see why Pavlov considered them so closely related. Certainly, the detailed interpretations that Pavlov offered for a variety of human syndromes have not gained widespread acceptance outside of his own country. For all that, Pavlov surely deserves credit for breaking the ground in applying studies of animal behavior to the problem of human disorders; and the interest he stimulated has led a number of other investigators to follow the same line of inquiry.

Studies at the Cornell Behavior Farm

Since Pavlov's death, further work in Russian laboratories has been bound rather closely to his original formulations; there is little evidence of the development of new approaches or fresh insights into the problem. In the United States, on the other hand, a much greater variety and independence of viewpoint can be found. The first workers to bring Pavlov's techniques to this country were Gantt at Johns Hopkins and Liddell at Cornell. Gantt had worked for several years in Pavlov's laboratory before returning to the United States and has since translated two volumes of Pavlov's writings into the English language. Although his own study of neurosis furnishes many interesting leads for future exploration, it is based almost entirely on the biography of one dog, "Nick," and qualifies more as a case history than as an experimental study [19].

Origins of Liddell's Work. Liddell and his associates at the Cornell Behavior Farm began their work with a study of the effects of the removal of the thyroid gland on the learning process in sheep. At first they used mazes, but these yielded no differences in learning scores between the normal and the thyroidectomized sheep. About 1926, therefore, Liddell turned to the conditional-reflex method developed by Pavlov. Where Pavlov, however, working with the dog, had used food to elicit the salivary response, Liddell, working with the sheep, substituted electric shock as a stimulus for flexing (retracting) the foreleg. At first it looked as if the new technique would prove quite successful; but to Liddell's surprise, one of his subjects, following an increase in the number of trials given per day, became so agitated in his behavior that he had to be discarded as a subject. Then in 1929 another case appeared in a sheep being trained on a relatively easy discrimination. This sheep began to show marked avoidance of the experimental situation. Out in the field he fled from the attendant coming to fetch him to the laboratory, dodging this way and that; on the way he had to be dragged along by brute force; once strapped into position in the conditioning harness, he pulled his legs up from the table, so that he hung suspended in the air; and if the straps were loosened to lower him, he struggled violently to get down to the floor. Two years later a third and a fourth case appeared, until still different circumstances [2].

Conditions Leading to Neurosis. By 1941, Anderson and Parmenter [3] reported the discovery of seven cases in a total experimental population of twenty-eight sheep. This contrasted with some fifty sheep that had been studied in the maze without turning up a single casualty. At this stage it seemed evident that the disturbance was evoked by *some* aspect of the conditioning situation, but it was not evident what feature of the situation it was. The neurosis had in each case arisen more or less spontaneously, and there was very little consistency from animal to animal in the events leading up to and immediately preceding the neurotic outbreak. In 1948, however, Liddell announced that he had localized one reliable method for precipitating a neurotic outbreak in both the sheep and the goat: "When 10-second signals inevitably reinforced with mild electric shock to the foreleg follow one another at constant intervals of 2 to 7 minutes, experimental neurosis results" [35, p. 182].

The Neurotic Pattern. A detailed description of the original neurotic pattern has been furnished by Anderson and Parmenter [3]. The most striking symptom, in most cases, is an oversensitivity or overreactivity to stimulation, accompanied by general restlessness and agitation; the neurotic sheep tends to respond more quickly to the conditional stimulus, to lift his leg farther and more vigorously, to respond more often between trials, and to react to stimuli that have not been paired with shock.

Physiological records show faster breathing, with sudden gasps and sighs, and sometimes a complete cessation for as long as 20 seconds. The pulse rate is higher and less regular and shows a greater acceleration to the conditional stimulus. Sometimes the neurotic sheep retain their urine and feces throughout the experimental session, only to expel them in copious amounts when the experimenter approaches to release them from the harness.

Outside the laboratory, the neurotic animals show larger "bursts" of activity, with quiet periods in between; on the whole, they are less active than the normal animals during the day but more restless at night. Out in the pasture, the neurotic sheep tend to avoid both the attendant coming to bring them to the laboratory and other members of the flock; they appear to be "shy" and fail to compete with other sheep for food. This pattern may be related to the avoidance of an unpleasant situation, including the human personnel, and a generalization of this avoidance to other animals.

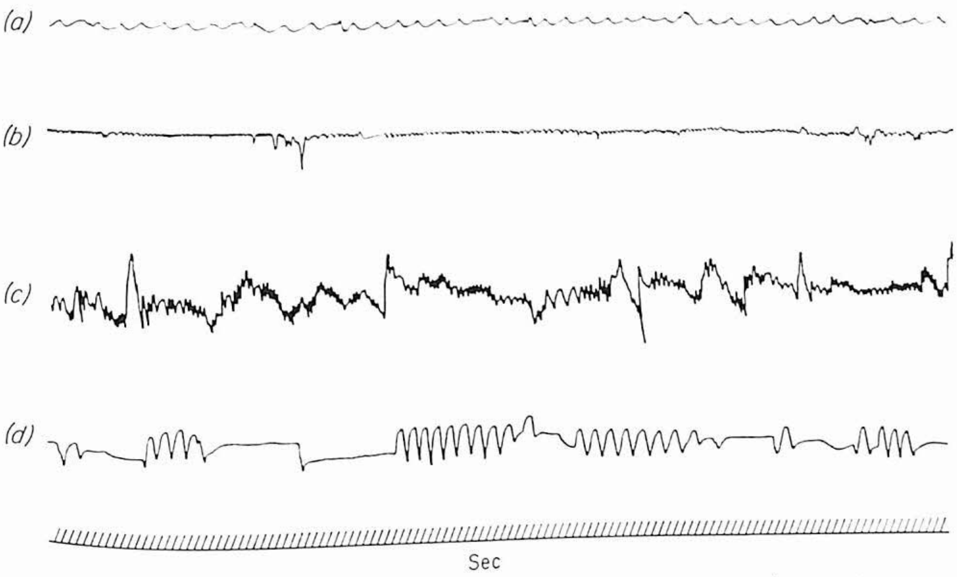

FIG. 10-1. Breathing records from a sheep: (*a*) before the onset of neurotic symptoms, (*b*) at first signs of neurosis, (*c*) irregular respiration symptomatic of neurosis, (*d*) prolonged pauses in breathing at a later stage in the development of the neurosis. [*From O. D. Anderson and R. Parmenter, A long-term study of the experimental neurosis in the sheep and dog. Psychosom. Med. Monogr.*, 1941, **2**, no. 5. *By permission of Hoeber-Harper.*]

A Second Type of Neurosis. In recent papers, Liddell indicates the above is the type of neurosis that develops when the interval between regularly spaced trials lasts for 5 minutes or longer. But when the interval is reduced to 2 minutes, quite a different pattern is observed [36]. The usually precise flexion of the foreleg at the signal gradually becomes stiff and awkward and finally gives way to its opposite, a rigid extension; at the end of the session the animal limps to the exit but thereupon recovers his usual freedom of locomotion. Liddell compares this to conversion hysteria in the human [33, 34]. The animal's general behavior during the session is tense, rigid, and mute, and his pulse rate remains low, even during the conditional signal.

The chief factor in precipitating either type of neurotic pattern, Liddell feels, is the mounting intensity of the animal's tension or "vigilance," summating from session to session. The difference between the two types of neurotic pattern, he suggests, may be related to "certain time constants of the central nervous system" [35, p. 185]. In the original agitated or hyperactive pattern, he feels, the sympathetic division of the autonomic nervous system may predominate, and, in the newly discovered inhibitory pattern, the parasympathetic division.

Neuroses Produced by Punishment

Pavlov and Liddell, who were primarily interested in physiology, stumbled across their first neurotic episodes quite by accident, while pursuing other lines of inquiry. More recent investigators, however, following the lead of Masserman [43], a psychiatrist, have tried to produce neuroses in animals by reproducing the conflict situation faced by the human neurotic. The first step in Masserman's technique was to train some cats to raise the lid of a food box in an experimental chamber and to eat specially prepared pellets of food; he then punished them with electric shocks or with jets of air as they were opening or about to open the box. Much the same technique has been used by Dimmick and his associates [9], Jacobsen and Skaarup [25], Watson [72], and Wolpe [76] with cats, by Lichtenstein [32] with dogs, and by Masserman and Pechtel [46, 47] with monkeys—using in this case a toy snake which was slipped into the food box on certain trials.

Reactions Observed by Various Experimenters. The first and most striking response noted by most of these investigators was one suggesting fear or panic, which some of them related to phobic reactions in the human. Wolpe, for example, found his cats showing such reactions as "rushing hither and thither, getting up on the hind-legs, clawing at the floor, roof, and sides of the experimental cage, crouching, trembling, spitting, [dilation of the pupils], rapid respiration, [erection of the hair], and, in some cases, urination or defecation" [76, p. 254]. Various reports indicate that the animals avoided the experimenter, resisted being put in the experimental apparatus, and made desperate attempts to escape. Most of the animals gave up eating from the food box, and many of them refused to eat elsewhere for extended periods.

Masserman also noted that some of his cats developed stereotyped responses to the situation, which he considered "counterphobic"; others engaged in preening, courting of attention, or aggressive behavior, which he classified as "regressive"; formerly active cats often became extremely passive; and one cat showed a "cataleptic type of resistance to manipulation" [43, p. 72].

Lichtenstein's dogs showed such reactions as turning the head away from the food box with a rigid posture "reminiscent of catatonia in humans" [32, p. 21], retching at the sight of food pellets, tremors and tics (including spontaneous flexions of the shocked leg, apparently similar to those observed by Liddell and his associates), and fighting with their cage mates. Lichtenstein calls particular attention to his finding that the symptoms often continued to increase in frequency and severity after the last of the shocks had been given, suggesting a two-stage process in which the observable manifestations were learned as a secondary reaction to an underlying process of "anxiety" or autonomic disturbance developed during the original pairing of the stimulus situation with the shock.

Masserman and Pechtel report that their monkeys failed to press the food-producing lever the required number of times to obtain the food but sometimes pressed an incorrect lever as many as a hundred times in rapid succession. (This is reminiscent of "displacement.") Startle and escape reactions occurred in response to lights or buzzers originally used to signal that food could be obtained, opening of the food box by the experimenter, and a variety of strange or sudden stimuli. When the monkeys ate, they often stuffed food frantically into their mouths. Diarrhea and loss of weight were common. Some monkeys showed "paranoid" levels of suspicion, occupying themselves "for long periods in minute, continuous, and repetitive examinations of every portion of their surroundings" [46, p. 261]. Two monkeys appeared to be hallucinating food, and acted as if they were eating it. Another pair showed "cataleptoid immobility." Motor coordination was greatly impaired, tics were common, and a variety of sexual deviations appeared.

Analysis of the Situation. Wolpe notes that some of the cats' reactions have been conditioned not only to the experimental situation as a whole but also to specific features that can be presented separately. Phobic reactions could be elicited by the entry of the experimenter into the animals' living cages, intensified by the presentation of the auditory stimulus that had accompanied the shock, or produced by stimulus generalization to the degree that other rooms in the building resembled the room in which the experiment had been conducted.

It is not clear how much of this picture really depends on the conflict induced by shocking the animal as he approaches the food. Wolpe, for example, gave a group of control cats several grid shocks without ever feeding them in the apparatus. He reports that they showed the same reactions as the rest of his cats except for the phobic reactions to the food pellets themselves. Watson, on the other hand, felt that his control cats showed clearer attempts to escape than his conflict animals did, with occasional immobility; and with repeated exposures, he found that the effect "wore off."

Watson also notes that continued training with the conflict procedure leads to a change in the animals' performance, in which they progress from the acute panic described by other observers toward a more orderly pattern of vacillation between the two competing responses. In this stage, "The cats alternately paced restlessly away from the food box and tensely and cautiously approached it. They checked their approach and alternated between a few inches of retreat and a few inches of approach, their eyes riveted on the food box. Some showed vacillation in regard to the pedal switch by an up-and-down motion of a hovering paw over the switch" [72, p. 341]. (The same pattern is observed in the rat [8, 10].) Later the conflict was usually resolved, either by resumption of eating or by abandonment of all attempts to approach the food box.*

Treatment of Experimental Neuroses

A question which naturally arises when neurosis is explored with animal subjects is whether remedial techniques can be found for the animal subjects which will suggest therapeutic measures for use with humans. In the early work by Pavlov and by Liddell the chief form of treatment attempted for the neurotic behavior, aside from pharmaceutical agents, was to release the animal from the experimental situation for a prolonged "rest cure." Usually, however, the symptoms promptly reappeared when the animal was brought back to the original situation.

Forced Contact. Masserman tried a variety of techniques to cure his animals. Among the more effective procedures were leaving the food box open in front of the animal, pushing him closer to the food with a movable barrier, or allowing him to become extremely hungry. Interestingly enough, these are also techniques which Masserman lists as means of accentuating the neurotic symptoms. By forcing closer contact with various of the key stimuli associated with the shock or the air blast, these procedures apparently evoke more frequent and more vigorous reactions and lead—in the absence of further air blasts or shocks—to faster extinction. Watson has accomplished much the same thing by manually forcing his cats to eat, and Dinsmoor [10] has shown that rats recover more rapidly from the effects of punishment if a high rate of responding is maintained by continued reinforcement.

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* Another recent finding which may be related to this type of experiment is Richter's [60] observation of "psychotic" behavior in several wild rats used in a study of the effects of ANTU (alpha-napthylthiourea) and other poisons used for exterminating purposes. The rats in question had survived sublethal doses of the poison and had learned to refuse poisoned food. In four cases reported by Richter, the rat developed an extremely unusual posture, spending almost his entire time for months on end "in one corner of [the] cage, half standing on [his] hind legs, half hanging with [his] forepaws from the wires at the top of the cage, and thrusting [his] nose up through the wires" [60, p. 198]. When forcibly placed in awkward postures, some rats tended to maintain them for several minutes without making any attempt to move (cataleptic behavior).

Gradual Adaptation. Superficially, Wolpe's mode of attack seems, in its gradual approach, almost the opposite of that used by Masserman. But it, too, depends on a process of extinction. In this case, the animals were exposed to stimuli that were similar to but not identical with the stimuli found in the original punishment situation, so that their panic reactions could be extinguished without ever reaching the original level of violence. Some animals were fed in rooms similar to the experimental room; others were fed at some distance from the source of the sound used as the feeding signal; and still others were given food immediately *after* the sound, on the assumption that the effects of the sound would by then be less intense. Essentially the same technique has been used by Kimble and Kendall [29] to reduce the frequency with which avoiding reactions occur in the rat during the extinction procedure.

Wolpe also reports that his cats could often be induced to eat again if the food were offered to them by hand; he feels that this procedure reinstates some of the features encountered in earlier, nonpunished feelings. Watson finds that stroking and petting sometimes lead to a resumption of eating.

"Working Through." Still another procedure has been illustrated by Masserman, with a second group of cats. These cats were trained to press downward on the edge of a circular plate or disk, which served as a switch to turn on the feeding signal (a light and a bell); when the signal came on, a pellet of food was dropped into the box. Again, shocks and air blasts were introduced. But when these stimuli were eliminated, he reports that "either spontaneously or under additional pressure from increased hunger or spatial restriction, [these animals] began once again to approach the switch, to re-explore its possibilities, and to manipulate it with increasing confidence until they had re-established their individual signal-sounding and feeding patterns. When this occurred, their neurotic abnormalities rapidly diminished and normal behavior returned" [43, p. 82]. Again, further contact leads to extinction of the neurotic reactions.

Comments on the Experimental Neuroses

The experiments we have reviewed under the heading of experimental neurosis have often been quite provocative and may furnish us with valuable leads for further exploration, but they do not seem to offer us very much help in understanding the processes at work in the neurotic personality. One of the difficulties may be the vagueness with which the word "neurotic" is defined. This is not entirely the fault of the animal investigators, since no one is sure exactly what the concrete criteria are for classifying even a human patient as neurotic and the practical criterion of seeking therapy cannot be applied to the animal subject. The result, however, has been an invitation to the imagination. Our interest in experimental neurosis has been derived in part from its relevance to an extremely serious social problem, the problem of how to deal with the ineffective and socially harmful behavior of the human patient. But it seems also to be derived in part from a rather childish and irresponsible delight in the bizarre and the mysterious. This delight may loom so large in our thinking as to convince us that any and all behavior that we do not understand is neurotic behavior. As Mowrer has remarked, "Sometimes it has appeared that the capacity for self-mystification on the part of the experimenter was the principal desideratum" [54, p. 510]. If neurotic behavior continues to be identified with the odd and the incomprehensible, it must remain—by definition—beyond the reach of our understanding. To the extent that the shrouds of mystery are torn aside, the process at work is divested of its occult glamour and is soon relegated to the world of normal, lawful behavior.

Lack of Experimental Analysis. Much of the difficulty, too, lies in a failure to take the word "experimental" seriously; the full power and vigor of an experimental analysis have rarely been applied. Replication of procedures is needed to distinguish the regularities from the accidents, and systematic variation of one factor at a time is needed to isolate the crucial factors embedded in a complex situation. But all too often the work on experimental neurosis has smacked more of the case-history approach than of the experimental method.

Finally, an associated difficulty lies in what we might call the "medical" bias. The necessity of locating the possibly separate causes of each feature of the subject's behavior has been ignored, and a variety of effects have been lumped together on the often doubtful supposition that they are all "symptoms" of a single underlying entity. But in practice these symptoms do not always seem to be closely related; Anderson and Parmenter, for example, point out that, "The symptomatology of the experimental neurosis . . . was found to be extremely variable—so variable, in fact, that variation must itself be considered symptomatic of the disorder. . . . In the present animal cases the symptom complex varied not only from one individual case to another but also in the same case from one day, week, or month to the next" [3, pp. 59 and 60]. Much the same description seems to apply to other work.

The merits of studying behavior as a whole in relation to the situation as a whole have been widely advertised, but if the attack on experimental neurosis is taken as a case history in scientific method, the conclusions seem quite damaging to the global approach. What we need to know is what specific procedure leads to what specific result. But what many of these investigators have studied is what collection of varied procedures leads, on occasion, to what varied collection of results. The remainder of this chapter, then, will be devoted to studies that have been concerned with the isolation of more specific relationships, rather than with neurosis as a whole.

BASIC PROCESSES

For many clinical practitioners it is almost an article of faith that some form of conflict between opposing "forces" or between incompatible sets of behavior lies at the heart of the common neurotic patterns. Most of the recent studies of experimental neurosis have also been based on this assumption. But some types of conflict appear to be quite innocuous, while others are more troublesome, even disastrous in their effect.

The Approach-approach Conflict. Reviewing the experimental work on conflict, Miller [49] has grouped it under three headings, each of which he illustrates by the behavior of a rat in a straight alley or runway. First, to establish an *approach-approach* conflict, the experimenter may reward the rat with food on successive occasions at each end of the runway. This should establish tendencies to run in both of these directions. No very lasting conflict will result, however, for as Smith and Guthrie [69] pointed out many years ago, even if a perfect balance could be achieved between the two opposing forces, it could not be maintained. The least vacillation in the rat's position or in his orientation toward either end of the alley would strengthen the tendency to go further in that direction. Miller compares the dynamic structure of this type of conflict to that of a pencil balanced on its point: the least sway in one direction or the other will lead it to topple.

The Avoidance-avoidance Conflict. The second type of conflict that Miller examines is that between two avoidance responses. Suppose that the rat is shocked at both ends of the alley, rather than given food. The dynamics of this *avoidance-avoidance* conflict, as Miller calls it, are different from the dynamics of the approach-approach conflict. Previously the subject was drawn to one end of the alley or the other. Now he seeks the middle, like a pendulum pushed off center, and here he reaches a stable equilibrium between the two opposing forces. The conflict is not readily resolved but tends to persist, suggesting that this type of conflict is more important than that between two approach responses; but Miller points out that if the rat were tested in a two-dimensional field instead of a one-dimensional alley, he would run off at right angles to the axis of the conflict. "Unless hemmed in, the subject should escape" [49, p. 443].

The Approach-avoidance Conflict. The third type of conflict, the *approach-avoidance* conflict, is the one that Miller considers most serious.

Here the animal has been both rewarded and shocked at the same end of the alley. (This is the type of conflict that has been employed in most of the recent studies of experimental neurosis.) If the avoidance tendency gains strength more rapidly than the approach tendency as the animal nears the goal (see Fig. 10-5), it may eventually match it in strength and block the animal from finally attaining the goal. In this case, there is no way for the subject to "leave the field," for the two tendencies remain inevitably aligned in precise opposition to each other wherever the animal may go, since both take their direction from the same goal. The subject remains trapped until one response or the other has been weakened by extinction. This may be why most psychotherapists are so doubtful of the desirability of punishment as a means of controlling behavior and why it is that Freud has personified this conflict as a contest between his two great metaphysical adversaries, the Id and the Superego.[*]

Avoidance

The importance of the avoidance-avoidance and particularly of the approach-avoidance conflict suggests that it would be worth our while to examine the dynamics of the avoidance process. This, moreover, will lay the foundation for later consideration of such important clinical mechanisms as repression, reaction formation, and displacement.

The clearest and most readily understood formula for producing avoidance behavior involves two stimuli: the first stimulus is relatively innocuous at the beginning of training and serves as a warning signal; the second stimulus is electric shock or some other stimulus from which the subject normally seeks to escape, and this is the stimulus to be avoided by the subject. The two stimuli are presented over and over again, with only a few seconds elapsing between the appearance of the warning signal and the administration of the shock. Whenever the subject makes the desired response in the interval between the two stimuli, however, the signal is turned off and the shock is omitted.

Theoretical Analysis. Since it is difficult to conceive of the omission of some event, such as shock, serving as a source of reinforcement (means of strengthening) for the avoiding response—many events are omitted following any given action—considerable controversy has developed among behavior theorists as to how this performance is maintained. Some writers have found it necessary to bridge the gap with hypothetical concepts of "expectancy," "anxiety," and the like. A concrete study of the observable relationships, however, indicates that the results may be explained in terms of a change in the role of the warning signal [12, 28, 62]. Through its pairing with the shock, the warning signal, too, gradually becomes aversive to the subject. Thereafter, any response that removes or reduces *this* stimulus or alters it in some way such that it is no longer followed by shock will be learned and maintained through the reinforcing effects of the change in stimulation.

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[*] Freud's third member of the *dramatis personae*, the Ego, may correspond to the process of discrimination in animal learning, whereby the animal learns to respond in one situation but not in another, thus "adjusting his behavior to the demands of reality."

This relationship can be demonstrated by isolating the two procedures, that of pairing signal with shock and that of terminating the signal when the animal responds, and utilizing them in separate stages of the experiment. This is illustrated in an experiment by Kalish [26]. In stage 1, a light-and-buzzer compound, analogous to the warning signal, was paired a number of times with electric shock. In stage 2, the animals were tested in a hurdle box. When they jumped the hurdle, the light and buzzer were turned off. The more times this stimulus compound had been presented with the shock, the more quickly the animals learned to jump the hurdle. The only change that is required to transform this study into a study of avoidance training is to use these two stages—pairing and termination—as alternative procedures on the same trial. Each trial begins with the presentation of the signal. If the subject fails to respond, the signal is followed by the shock (pairing); but if the subject does respond, the signal is turned off (termination), and no shock is given in its absence.

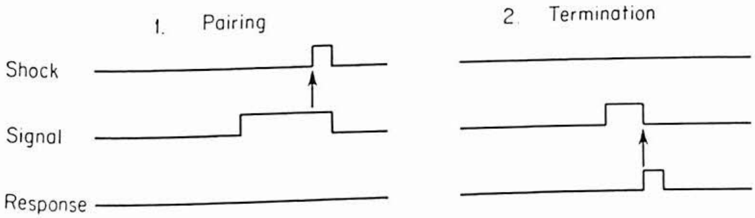

FIG. 10-2. A schematic diagram of the alternatives available on each trial during avoidance conditioning. (1) If no response occurs, the signal is followed by shock. (2) But if the animal does respond, the signal is turned off before the shock appears.

Notice that many of the symptoms observed in recent studies of experimental neurosis involve similar behavior of withdrawing from signals that have been paired with shock or other "traumatic" stimuli. This behavior, plus internal physiological disturbances, seems to make up the bulk of the "phobic" symptoms that have been described by various observers. The same pattern of events may also account for many of the phobias encountered in human patients.

Avoidance without a Signal. Other versions of avoidance provide analogies for some of the "underlying" conflicts in human neurosis. In these procedures the warning signal is not presented by the experimenter but must be provided by the animal himself. As our first example, we shall take the situation where some response, such as pushing down a bar or pedal projecting from one wall of the experimental box, turns off the disturbing stimulus but where the stimulus reappears whenever the bar is let up again. The "down" part of the response is reinforced by termination of the stimulus, and the "up" part is punished by its return. As with the chronic defensive postures of some of our psychotic patients or the inhibitory muscular tensions of the neurotic [22, 59], the rat learns to maintain the "down" response over long periods of time [21]. A detailed analysis of the variations in pressure exerted by the animal in this type of situation shows that tentative, partial releases of the response mechanism are commonly followed by sharp, forceful restorations of the maximal reaction [75]. Apparently the stimuli arising inside the animal as he begins to let up his pressure serve as adequate warning signals for the punishment that will follow, and the animal learns to remove them by returning to his defensive maneuver with renewed vigor. Compare this internal stimulation with the feelings of anxiety reported by human patients when they relinquish their habitual defenses for a time.

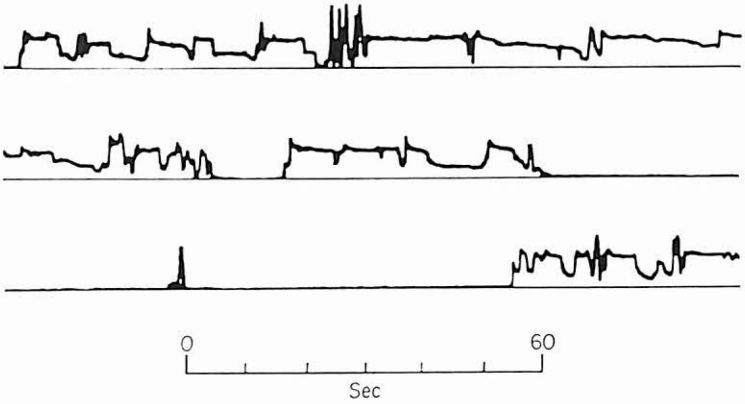

Fig. 10-3. A continuous record on moving tape of the rat's displacement of a panel set in one wall of his experimental box. Gradual releases of pressure, which almost allow the record to drop to the base line and the aversive light to reappear, are often followed by sharp rises, representing sudden restorations of pressure. [*Three segments of a record from W. A. Winnick, Anxiety indicators in an avoidance response during conflict and nonconflict. J. Comp. Physiol. Psychol.*, 1956, **49**, 52–59.]

Another form of avoidance that requires no external signal involves repeated responding by the subject to "stave off" the undesirable state of affairs. This procedure has been explored in a number of studies by Sidman [e.g., 65, 66]. Electric shocks are imposed at regular intervals when the subject does not respond, but each occurrence of the appropriate response is followed by a brief period of relief, when no shocks are given.

Here again the self-stimulation produced by making the avoiding response seems to be sufficiently distinctive to the animal to provide an effective (reinforcing) change from the patterns of stimulation produced by other forms of activity, all of which are eventually accompanied or followed by shock. The animal might be said to make the appropriate response to "keep from doing something else." Compare this with the ritualistic compulsions—e.g., counting—of many a patient observed in the clinic. Compare it also with the diffuse hyperactivity of the manic patient.

Anxiety

In analyzing the role of the warning signal in avoidance training we saw that stimuli that are paired with shock become aversive to the subject, so that their termination can be used as a means of reinforcing appropriate behavior. Another function of such a stimulus, according to some views, is to serve as the conditional stimulus for a hypothetical response known as "fear" or "anxiety." Concerning the effects of this anxiety on the subject's behavior, however, there are two main schools of thought.

Anxiety as a Depressive State. The first view, following Estes and Skinner [16], holds that anxiety is inherently depressive and will reduce the level of the subject's activity. This viewpoint has considerable empirical support, for in most cases the observed effect of stimuli that precede shock is to disrupt whatever the animal has previously been doing. This depressive effect has been used as an index to the strength of the anxiety, and various experimenters have tested the effects of drugs [23], electroconvulsive shock [5], and other therapeutic measures [20] on this index. Other writers, however, have argued that we can account for the observed disruption of the recorded response without calling up such an *ad hoc* mechanism [1, 13, 27]. It is difficult in laboratory studies of this kind to deliver the stimulus to the subject in such a way as to eliminate the possibility that he may find unintended means of reducing or eliminating the stimulation. Visual stimuli may be avoided by turning the head or closing or shielding the eyes; auditory stimuli usually vary considerably in intensity in various parts of the experimental chamber; shock is frequently reduced by adopting special postures ("freezing") or gaits on the grid; and these avoiding responses are frequently incompatible with the response that is being recorded by the experimenter.

Anxiety as a Drive. The second school classifies anxiety as a drive. Like other drives, anxiety is assumed to have energizing properties and to increase, rather than to decrease, the animal's level of activity. To explain the apparent negative evidence, this school may appeal to the interfering responses mentioned above [1] or may argue that the behavior that is energized by this drive is often the behavior of doing nothing [17]. This last argument seems peculiarly difficult to test, since it is difficult to tell in a given case whether we should expect an increase or a decrease in activity.

A further implication that is usually attached to the classification of anxiety as a drive is that any performance that reduces or eliminates the anxiety will be reinforced—this is used to explain the learning of avoiding responses. But the elimination of the anxiety occurs through the removal of the stimulus that arouses it (the warning signal), and the effect which the anxiety drive is summoned to explain can be handled with equal facility in terms of the event that is actually observed, i.e., the change in stimulation [13, 28, 62]. If, then, the reduction in anxiety is merely a hypothetical accompaniment of the observable change in stimulation, we wonder whether this member of the crew can be earning his passage.

In an effort to lend corporeal substance to this variable, Solomon and Wynne [71] have recently proposed a much more explicit identification of anxiety with diffuse patterns of neural, muscular, and glandular activity elicited directly by the conditional and unconditional stimuli. This treatment may serve to add testable implications to the term by linking it with known facts of physiological functioning. Solomon and Wynne suggest, for example, that when the subject is permitted to avoid the shock by responding to a signal, he may remove the anxiety-eliciting signal before the slow-moving physiological pattern has time to occur. When the anxiety reaction does not occur, there is no reason why it should extinguish, and it is suggested that the resulting "conservation" of the anxiety may account in part for the prolonged resistance sometimes shown by avoiding responses to experimental extinction [70]. But if anxiety is to be transformed from ectoplasm into protoplasm and enter the real world, as it were, it is obvious that considerably more data will be needed to analyze the way in which these internal patterns interact with more readily observed behavior.

Punishment and Repression

Although other procedures can be arranged for laboratory studies, the chief source of approach-avoidance conflicts in natural settings is the punishment of previously or concurrently rewarded behavior. For many years psychologists viewed punishment simply as the opposite of reward in its action, as a direct means of reducing the strength of whatever connection between the stimulus and the response might have been established by earlier reinforcements. Today, however, punishment is commonly regarded as a means of setting up opposing or inhibiting responses that hold the original behavior in check but which do not necessarily remove it from the organism's repertoire.

Suppression and Recovery. As the subject proceeds with the sequence or chain of actions that leads to punishment, he meets many successive sets of stimuli, some produced by the change in external stimulation, others arising inside the body as a direct product of the movements themselves. Each new group of stimuli sets the occasion for the next response in the series. But when punishment is encountered, these stimuli acquire an additional function. Whenever the animal responds to these stimuli in the usual fashion, he causes them to be followed by the punishment. These stimuli, then, are *paired* with the punishment; they become warning signals, and any behavior that prevents the punished response from occurring serves as an avoiding response and is reinforced by the accompanying alteration in these warning signals [12, 13]. This means that the punished animal is not merely quiescent but is in a state of conflict and that the punished behavior may burst forth again when the punishment has been lifted and the avoiding responses have extinguished.

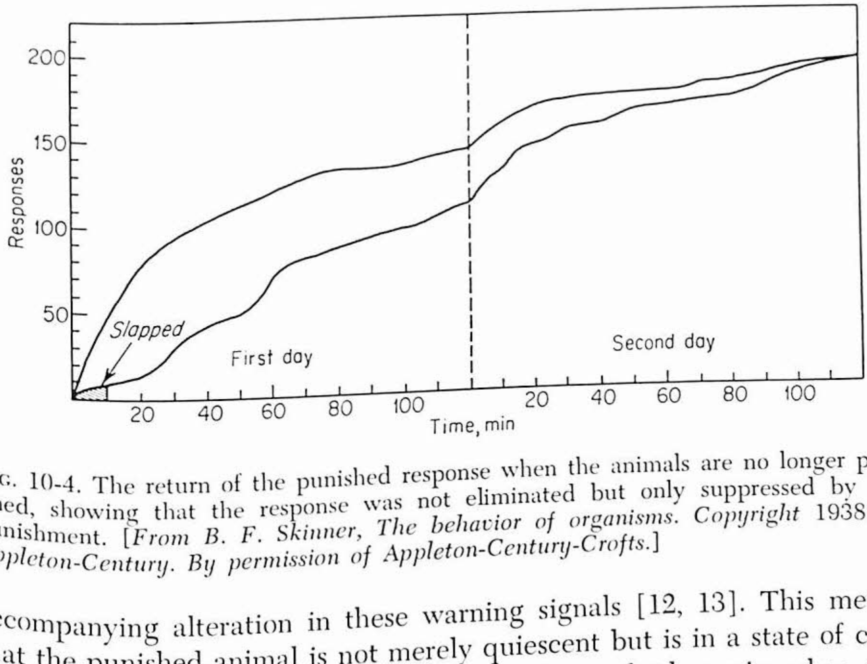

FIG. 10-4. The return of the punished response when the animals are no longer punished, showing that the response was not eliminated but only suppressed by the punishment. [*From B. F. Skinner, The behavior of organisms. Copyright* 1938 *by Appleton-Century. By permission of Appleton-Century-Crofts.*]

The reappearance, without further reinforcement, of a response that has been suppressed by punishment has been demonstrated by Skinner [67, pp. 154 and 155]. His rats were originally trained to press a bar to obtain food, then were put on an extinction procedure, with no more food forthcoming. During the first part of the extinction period the rats were slapped by a mechanical device whenever they pressed the bar, and this led to a substantial depression in their rate of responding, as compared with control rats that were not punished. When the experimenter stopped punishing the animals, however, their rate of pressing increased again and for a time became higher than that of the control rats. By the end of two sessions the recovery was complete, in the sense that the punished rats had responded as many times as their nonpunished controls. Estes has also obtained the same results, using shock rather than slapping as the punishing stimulus [15, exp. A]. In these experiments it looks as though the response must have maintained a hidden strength throughout the period of punishment, even though this did not manifest itself until after the punishment was over, for the rate of responding increased again without any further reinforcement having been provided.

Clinical Parallels. To the student of human behavior in the clinic many parallels will be obvious. For example: when certain actions, including recalling or thinking about certain things, characteristically lead to painful consequences, they are said to be "repressed." The patient ceases to remember or think about these events; yet such responses are not wholly lost, for they, like the bar presses that have been followed by shock, can be recovered. When the therapist or the patient himself in carrying through his chains of behavior or "association" produces the stimuli for these repressed responses, inhibitory or distracting avoiding responses may appear. Here the clinician speaks of "resistance," an active process employed to prevent the disturbing thoughts from recurring. The clinician carefully avoids any further punishment for the associations leading to the repressed material, in the hope that the effects of previous punishments will gradually dissipate (become extinguished) in this "permissive" situation [63, 64]. Positive reinforcement in the form of social approval is sometimes presented for responses that seem likely to be significant, or even if no such policy is followed, the therapist's interest or attention may play a similar role [30]. Such reinforcements encourage more frequent self-stimulation and should, if we can rely upon laboratory findings [10], speed up the extinction of the avoiding reactions and free the patient of his repressions. Various drugs may be employed which apparently reduce the strength of the avoiding reactions for a time [4] and permit the therapist to uncover and inspect the repressed material. On the other hand, if the patient's anxiety or resistance becomes too violent or if there is some danger that he may leave therapy, it may be desirable to "creep up" on the repressed material more gradually—that is, to eliminate the avoiding reactions without frequently evoking them.

Toleration Method. An analogy for this technique can be found in the therapeutic procedure studied by Wolpe (described earlier in this chapter) or in some findings by Kimble and Kendall [29]. These men trained their rats to avoid an electric shock by turning a small wheel whenever a fairly bright light came on as a warning signal. The animals were then divided into two groups. The control animals were extinguished in the usual manner: the light was turned on for 15-second intervals, with no shock, and the number of times the animal turned the wheel was recorded. The experimental animals, however, were extinguished by the "toleration" method. A very dim light was turned on and gradually increased in intensity. Apparently the dim light was not sufficiently similar to the original warning signal to evoke very many avoiding responses. Yet continued exposure to the light at low intensity seemed to reduce its effectiveness even at higher intensities, for these animals made far fewer avoiding responses when the light was finally raised to its original value. The conclusion of this experiment, if our parallel is correct, is that the therapist may circumvent his patient's resistance by presenting him with carefully graded dosages of the stimuli he is trying to avoid. More time will be required, but if the process is sufficiently gradual, much less resistance should be shown.

SPECIAL MECHANISMS

Reaction Formation

One of the interesting features of Miller's analysis of the approach-avoidance conflict, reviewed earlier in this chapter, is that the immediate vigor of the avoiding reactions should rise and fall with changes in the strength of the approach response [49]. This relationship can be seen in Figure 10-5. Suppose, for example, that the over-all strength of the animal's approach response has been raised by further reinforcement or some other factor from the level of the lower broken line to that of the upper broken line. If this represents behavior in a conflict alley, for example, the animal will now move closer to the goal before he is stopped by the opposing avoidance reaction, as represented by the solid line. The two responses reach a new equilibrium at the point of intersection S, a point much closer to the goal than the old point of intersection W, and a point which is much higher in terms of the immediate strength of both responses. Thus, the higher level of the approach response brings the animal closer to the goal, where the counterbalancing avoiding reaction is also much stronger.

Clinicians have long recognized this relationship and have given it the name of "reaction formation." Frequently they infer the hidden existence or the strength of behavioral tendencies they cannot observe from the vigor of the opposing reactions that they can observe. Even when the patient himself cannot distinguish these tendencies in his behavior, the opposing avoidance reactions are believed to attest to their existence.

So far, the relationship is a fairly simple one. But some writers believe that reaction formation is properly illustrated only when the net result of the opposing forces takes the subject farther and farther *away* from the goal as the circumstances become more and more appropriate for an *approach* to the goal. Although there seems to be no experimentally derived theory of behavior that would predict this result, Mowrer, for example, seems to feel that he has found such a relationship [53, 54]. In the experiment in question, Mowrer first trained his rats to press a pedal to turn off a shock of gradually mounting intensity which was delivered through a floor grid. Then the pedal was itself electrified through a separate circuit. "After discovering that the pedal was charged," he reports, "these animals would frequently *retreat* from the pedal end of the apparatus soon after they began to feel the grill shock, i.e., as soon as they began to have an impulse to press the pedal. In effect, they were thus running away from the pedal because they wanted to go forward and touch it" [54, p. 386]. Masserman has reported similar observations [43].

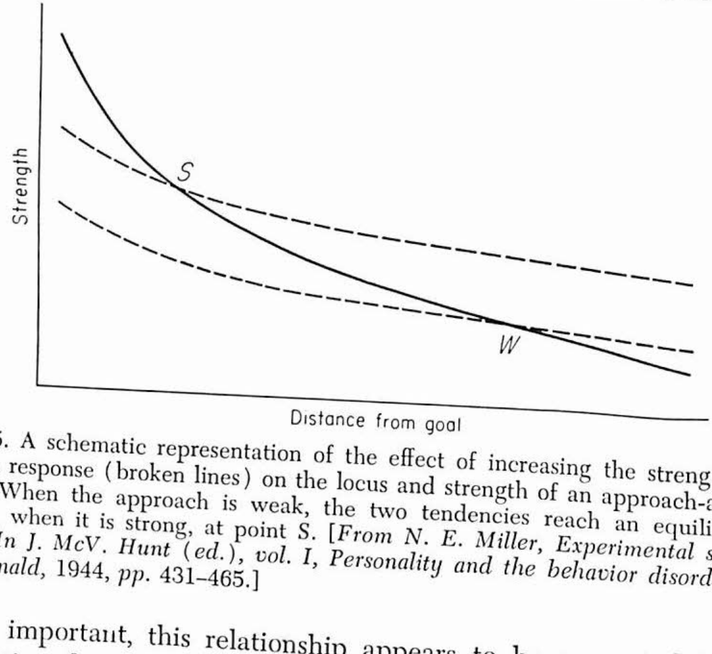

FIG. 10-5. A schematic representation of the effect of increasing the strength of the approach response (broken lines) on the locus and strength of an approach-avoidance conflict. When the approach is weak, the two tendencies reach an equilibrium at point *W*; when it is strong, at point *S*. [*From N. E. Miller, Experimental studies of conflict. In J. McV. Hunt (ed.), vol. I, Personality and the behavior disorders. New York: Ronald,* 1944, *pp.* 431–465.]

More important, this relationship appears to be supported by some quantitative data collected by Phillips and Hall [58]. These authors used an 18-foot alley with a starting box at one end and a goal box at the other. After first training their rats to run down the alley to get food, they began giving them shocks in the goal box. Once the conflict had been established, the authors varied the strength of the approach response by varying the length of time for which the rats had been deprived of food (hunger drive) before they were placed in the alley. The results they obtained appear to be quite contrary to current analyses of approach-avoidance conflict, as illustrated in Figure 10-5. For although some of their measures are not clearly specified, Phillips and Hall report that as they raised the level of hunger their animals (*a*) took longer to leave the start box, (*b*) showed their first hesitation earlier in their path toward the goal, and (*c*) approached *less* closely to the goal than when their level of hunger was lower. (The opposite results were obtained with this measure by Miller, Brown, and Lipofsky, according to Miller [49].) If these seemingly paradoxical results can be duplicated by other experimenters, they will provide a serious challenge to previous analyses of the conflict situation.

Displacement

Despite variations in the exact meaning given to the term, the general idea that responses may be "displaced" from one stimulus object to another is a familiar one to social and clinical psychologists. In its simplest sense, the term merely implies that a response appears or increases in strength in a situation that is different from the one in which it was originally learned and to which it is really appropriate. In animal research this is commonly known as stimulus generalization. To illustrate the relationship, Miller [50] once trained some rats to strike at each other, as if boxing; when only one rat was put in the box with a celluloid doll substituted for his partner, the rat struck at the doll.

Displacement of Punished Responses. A more complex relationship is implied when the term refers to the displacement of a response that has been suppressed in the original situation by punishment or by the threat of punishment. In this case, it must be assumed that there is a greater generalization of the displaced response than there is of the avoidance reaction that holds it in check. In other words, there must be a difference in the slope of the curve relating the strength of each response to the degree of similarity of the new stimulus (gradient of generalization). This too may be illustrated by Figure 10-5, if the term "distance" is now interpreted as distance from the original situation along some stimulus dimension.

Murray and Miller [55] have demonstrated the possibility of such a difference in generalization in the runway, using the strength of the rat's pull against a restraining harness as their measure. Rats trained to run down one alley to get food pulled almost as hard when tested in another alley of different color and width as they did in the original alley. But rats originally trained to run down the alley to escape from shock showed much less generalization from one alley to the other (when tested in the absence of shock). Murray and Miller believe that the weak generalization shown by the second group is typical of avoidance behavior in general. In a subsequent paper [52] they have explored the reasons for this difference, but their argument seems to rest on some rather questionable assumptions.

Using the same type of apparatus, Miller and Kraeling [51] have demonstrated displacement itself. The authors first trained their rats to run down an alley to obtain food; next they gave the animals electric shock whenever they opened the food receptacle, until they learned to refrain from taking the food. One group was then tested in the original alley, another in an "intermediate" alley differing in color and width, and the third in an alley differing still more from the first. "When the test alley was the same as the training one," they report, "only 23% of the Ss reached the goal during the test trials. In the intermediate and different alleys progressively increasing percentages, 37% and 70%, reached the goal" [51, p. 219].

Displacement as a Continuing Process. A technique for the study of displacement as a persisting state of behavior has been developed in a series of experiments by Dinsmoor [10, 11] and Cook and Dinsmoor [8], using the bar-pressing apparatus. An overhead light could be turned on or off to represent two different stimulus situations. Tests were conducted to determine the degree to which behavior generalized between these two situations following differential reinforcement, differential punishment, or a combination of the two. In the first of these experiments [11], the rats were reinforced with food for some of the responses they made when the light was on, on a random time schedule, but were never given food in the dark. When they had learned to make some 85 to 90 per cent of their responses in the light, the experimenter tested their performances at various levels of hunger. The total number of presses shifted considerably from one extreme to the other, showing that the *height* of the gradient of generalization could be raised or lowered almost at will. But the *slope* of this gradient was not affected, for the *proportion* of the responses occurring under either of these stimulus conditions remained the same at all levels.

In the second experiment in this series [10], the rats received food in both light and dark but were punished with shock each time they pressed in the dark. One of the factors varied in this experiment was the intensity of the shock, and this affected not only the height of the gradient of generalization but also its slope. When the severity of the shock was increased, the rats reduced their rate of pressing in the dark from about one sixth of that in the light to about one twentieth.

Finally, in the third experiment, conducted by Cook and Dinsmoor [8], the procedures of selective reinforcement and selective punishment were combined. First the rats learned to respond in the presence of a positive stimulus compound of light and silence for food and to give up their responding in the dark with a tone sounding. Once their performance had stabilized on this schedule, they were given a strong electric shock whenever they pressed the bar in the presence of the positive stimulus. One result, of course, was that the total number of responses suffered a considerable decline. But the other result was that the animals now responded mainly in the dark instead of in the light. Over several hours of testing, 85 per cent of all presses occurred in the "inappropriate" situation, where no food had ever been received. The authors suggest that this offers a reasonable analogue for clinical displacement but feel that additional work is needed to analyze the "psychodynamics" (functional relations) of the situation more fully.

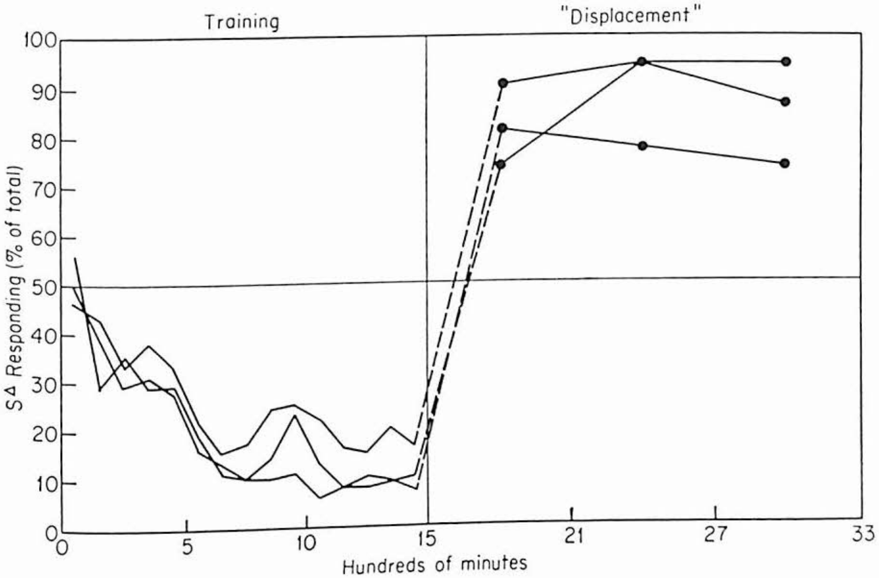

FIG. 10-6. Percentage of responding occurring in the inappropriate situation (S$^\Delta$). The percentage declines during discrimination training, since no reward is provided, but rises to some 85 per cent of the total when responding in the appropriate situation is punished as well as rewarded. [*From D. A. Cook and J. A. Dinsmoor, A laboratory model for the study of displacement. Paper read at East. Psychol. Ass., New York, April,* 1954.]

Addiction

A possible functional model for human addictions to alcohol and other disinhibiting drugs is suggested by some work conducted by Masserman and Yum [48]. In a study of the influence of alcohol on experimental neuroses produced by Masserman's air-blast technique (reviewed earlier in this chapter), these authors found that injection by the experimenter or ingestion by the animal of moderate amounts of alcohol led to a resumption of switch manipulation, eating, and a "mitigation of phobias, motor disturbances and other neurotic patterns" [48, p. 49]. Although the cats had normally shown a definite preference for plain milk over milk "spiked" with 5 per cent alcohol, animals that "had experienced relief from neurotic symptoms during previous artificially induced intoxications showed a definite tendency to take alcohol-milk spontaneously" [48, p. 50].

After they had reestablished their normal behavior patterns, however, they gradually gave up the alcohol again, indicating that no physiological "craving" was involved.

Ulcers

If sufficiently prolonged, the procedures we have been discussing under the headings of conflict, avoidance, and anxiety may cause structural damage to the organism. Mahl [38] has shown that the gastric secretion of hydrochloric acid increases markedly in dogs that are exposed for long periods to "chronic fear" (presentations of a buzzer sometimes followed by severe shock). Following this up, Weisz [73] found that both "fear" and "conflict" (in combination with an empty stomach) produced significant increases in the number of rats showing gastric ulcers. The rats in the "fear" group were repeatedly exposed to a light that was sometimes followed by shock, while the rats in the "conflict" group had to move onto a charged grid in order to eat or drink.

Much the same conflict situation, with a new set of control groups, was used by Sawrey, Conger, and Turrell [61]. They found that a combination of food deprivation and simple exposure to shock would produce ulceration in 30 to 40 per cent of their rats within thirty days, but that the addition of a conflict between consummatory and shock-avoiding behavior raised this figure to 76 per cent.

Brady, Porter, Conrad, and Mason [6] paired monkeys required to press a lever to postpone shock with "yoked" control monkeys connected to the same shock circuit. Whenever the experimental monkey failed to make the avoiding response, both monkeys were shocked. When the experimental monkey died, the control monkey was sacrificed and both were subjected to complete post-mortem examination. The avoidance monkeys each showed "extensive gastro-intestinal lesions," but none of the control animals, despite identical exposure to the shock, "showed any indications of such gastrointenstinal complications" [6, p. 72]. It is clear that the key factors producing the ulcers in these studies are not yet well isolated, but the evidence for the effectiveness of the general type of variable we have been considering is quite convincing.

Fixation

One of the striking things about neurotic manifestations in the human patient is the way in which many of these responses outlive their usefulness and persist when no source of reinforcement is apparent or when alternative modes of action would seem far more effective. Although hidden sources of reinforcement may explain many of these instances, the topic has held considerable fascination for the animal experimenter. Recent examples are the prolonged resistance to extinction following intermittent schedules of food reinforcement found by Skinner [68] and the difficulties faced by Solomon, Kamin, and Wynne [70] in extinguishing the hurdle-jumping response in dogs following "traumatic" avoidance training. Some of the most extensive and most controversial work in this area is found in a program of studies conducted by Maier and his students at the University of Michigan [e.g., 39, 40, 41, 42].

Maier's Procedure: the Insoluble Problem. For this work, Maier used a relatively complex type of apparatus known as a jumping stand. "The essential feature of the technique is to require the animal to leap from a jumping stand at cards placed in the two windows cut in an upright screen." These cards bear distinctive visual patterns, such as a white circle on a black background and a black circle on a white background. The cards "may be latched or unlatched. If the unlatched card is struck it falls over and the animal gains access to food placed on a platform behind the window, but if the latched card is struck the animal receives a bump on the nose and falls into a net below" [42, p. 522].

In the usual discrimination training procedure, one figure is designated as correct, and this card is randomly shifted from left to right to prevent the rat from learning to base his choice on position alone. Maier, however, makes the problem completely insoluble to the rat by selecting the card as well as the position at random; regardless of which figure or which window the rat chooses, he will succeed on half of his trials and will be punished (by the bump and the fall) on the other half. Under this procedure a few of the rats settle on one or the other of the stimulus cards, but the vast majority form a stereotyped position habit, always jumping to the left or always jumping to the right. The strength of the rat's fixation on the position habit is then tested by presenting him with the standard discrimination problem, which the rat *can* solve if he follows the correct stimulus card as it shifts from side to side on successive trials. Most of the rats, however, are very slow to abandon their stereotyped preference even after many trials on the new problem. Thus, they show fixation, according to Maier.

Analysis of Maier's Procedure. Maier's procedure is quite complicated, of course, since it involves two stimulus patterns, two positions, intermittent reward, intermittent punishment, another form of punishment for delay in jumping, and the possibility of making abortive jumps that strike neither stimulus card in the proper manner. Maier himself attributes the rats' fixation to the "frustration" resulting from the insoluble problem and the punishment received on 50 per cent of the trials. The generality of this relationship, however, seems rather limited, for similar fixations do not ordinarily appear in other experiments where insoluble problems have been presented or where frequent punishment has been given.

Intermittent Schedules. Wilcoxon [74] has argued that it is the intermittent schedule of reward and punishment that is primarily responsible for the fixation and that the problem need not be made insoluble. In his procedure, one window leads to reward on half of the trials and to punishment on the other half, giving an intermittent schedule for both; since the other window always leads to punishment, the problem may be regarded as soluble. Wilcoxon finds that this problem leads to quicker adoption of a consistent position habit than Maier's does and yields a higher percentage of fixations within the group.

Abortive Jumping. Wilcoxon has also pointed out that many of the animals exposed to the insoluble problem learn to jump in an abortive manner; that is, they jump to the left or to the right of the cards, hit them broadside rather than head on, or jump too lightly against them to knock them over. These maneuvers protect the animal from the punishing effects of bumping his nose and prepare him for the fall into the net. Wilcoxon finds that the animals that learn abortive jumping during their original training are less likely than other rats to learn the subsequent test discrimination, indicating that the abortive jumping is one of the factors that interfere with the learning of the correct responses.

No Punishment Necessary. Lauer and Estes [31] have gone even further than Wilcoxon, showing that no form of punishment is necessary to produce stereotyped position habits in the jumping stand. In their work, neither door was ever locked and no rat was ever punished by a fall into the net. During sixty-two days of preliminary training, each rat was given hand-guided trials interspersed with free trials until on a given day he had jumped at least twice through each window on the free trials. During four series of acquisition and four series of extinction trials, the last extinction series numbering over 200 trials, fourteen of their fifteen rats never deviated from their initial position preference, and the remaining rat made but one switch.

Two Distinct Groups. A major basis for Maier's feeling that the relationship he is studying is a highly special phenomenon, unrelated to the commonly recognized laws of behavior, is that his rats fall into two distinct groups [40]. Some of them, he points out, learn the discrimination task in less than a hundred trials, following their exposure to the insoluble problem. The majority, however, continue their position preference for at least 200 trials, at which point Maier ends the test. Since there are relatively few intervening scores, the animals seem to form two separate groupings, the nonfixated and the fixated. This leads Maier to postulate the existence of a threshold for frustration which varies in its level from rat to rat. Those with relatively low thresholds may pass over the threshold, become fixated, and maintain their position habits for many trials; those with relatively high thresholds may never become fixated and may continue to perform in a normal fashion. Yet from the truncated data that Maier has obtained, it is difficult to guess whether the complete distribution of scores would actually show a separation of the rats into two groups or whether it is merely extremely skewed, with a peak at the lower end and a long tail at the upper. Interestingly enough, in the one case where Maier does present a complete distribution of scores, using a modified test procedure which hastens the learning of the subsequent discrimination, the distributions are clearly skewed and not bimodal [41].

Inconsistency of This Type of Fixation. Finally, Maier bases much of his argument for the abnormal nature of the fixations he has produced on the contrast between the animals' failure to shift position and their success in reacting differentially to the positive and negative stimuli when they appear on the chosen side [40]. The animals show greater resistance to leaving the jumping platform, for example, when the negative stimulus appears than when the positive stimulus is present. They have to be forced off the platform by prodding with a pointed stick, tapping the tail, electric shock, or blasting with successively stronger jets of air. Similarly, they often learn to jump abortively to the negative stimulus, while jumping in the normal fashion to the positive stimulus. Since the rats do show these differential reactions to the two stimulus cards when they are on the fixated side, Maier feels that they should also learn to jump to the nonfixated side and finally to jump to whichever side has the positive card on each trial. Their failure to do this, he maintains, demonstrates the rigid, compulsive nature of their fixation. But unless we postulate some anthropomorphic process of knowledge or understanding on the part of the rat, it is difficult to see why one type of behavior *should* necessarily lead to the other. Discrimination between two cards and jumping to the nonpreferred side may be entirely unrelated items of behavior. And once the animal does make his initial jump to the opposite side, the subsequent discrimination develops very rapidly.

What Maier has not recognized, moreover, is that the rats' success in this aspect of their learning vitiates his entire interpretation. If the fixation is due to frustration, presumably a generalized state of the organism, why should this fixation be limited to one aspect of the subject's behavior? Furthermore, when Maier attempts to extend his theory to social movements or to the behavior of neurotic patients [39], the question arises as to how we may determine what behavior should show fixation and what behavior should not. To date, no rules have been offered for making this prediction.

Regression

In some cases, the pattern of behavior shown by a maladjusted or psychotic individual seems more suitable to an earlier stage in his development than it does to his current circumstances. The child acts like an infant or the adult like a child. In clinical cases, where the history of the behavior may not be clear, it is difficult to tell whether this is simply a mode of action that has never been "outgrown" by the acquisition of new skills, whether it represents a means of dealing with some special problem faced by the individual, or whether it really represents a return to an earlier pattern of performance, as is assumed by the use of the term "regression." But in any case, students of animal behavior have demonstrated that it is quite easy to *produce* a return to an earlier mode of behavior by weakening the later response through punishment or extinction.

Regression Produced by Punishment. In an experimental demonstration of regression produced by punishment, Mowrer [53] used two groups of rats. The experimental animals were put on a low-voltage shock grid, where they learned to sit up on their haunches, with their forepaws in the air, presumably because this minimized their area of contact with the grid. This was the first response they learned to the shock. Later, these animals, along with some control animals that had not been trained to sit on their haunches, were taught to turn off the shock by pressing a pedal mounted at one end of the box. Finally, the pedal itself was electrified, so that the animal also received a mild shock when he approached the pedal to turn off the shock through the floor. The animals in the control group continued to press the pedal during this final test session, despite the punishment, but four of the five experimental animals "regressed" to the earlier response of sitting on their haunches.

Regression Produced by Extinction. Regression by extinction in the cat has been demonstrated by Masserman [44, p. 118] and in the rat by Carey [7]. Carey trained his rats to press a bar twice in rapid succession, less than a quarter of a second apart, to procure food. He gave his subjects 3,000 reinforcements for these "doubles," as he called them, spread over forty-eight days of training. This was the first mode of response. Next, he trained the same animals to press the bar only once before turning to the food tray to seize their pellet. He gave 1,500 reinforcements to this response. Finally, he withheld all food from the animals to extinguish the single-press response. At this point, he observed an increase in the number of "doubles" produced, even though this was more difficult and more complex than the later mode of action. As a control measure, Carey also trained another group of animals first to make a single press, then to make doubles. As before, when the doubles were subjected to extinction, the single presses returned in strength.

Masochism

Earlier in this chapter we considered the normal action of punishment and saw how it led to the suppression of the punished response. But does intended punishment always work in this way? Clinical evidence suggests that some people "enjoy," or at least seek out, normally unpleasant or painful experiences. Is this a real phenomenon, and can it be reproduced by specified procedures in the laboratory in the same way that the chemist synthesizes compounds originally found only in nature? Considerable attention has been devoted in laboratory studies to procedures for establishing a neutral stimulus as a secondary reinforcer—that is, giving it the power to strengthen behavior. The remaining question is whether a stimulus that is inherently aversive, or even painful, can also be given reinforcing properties.

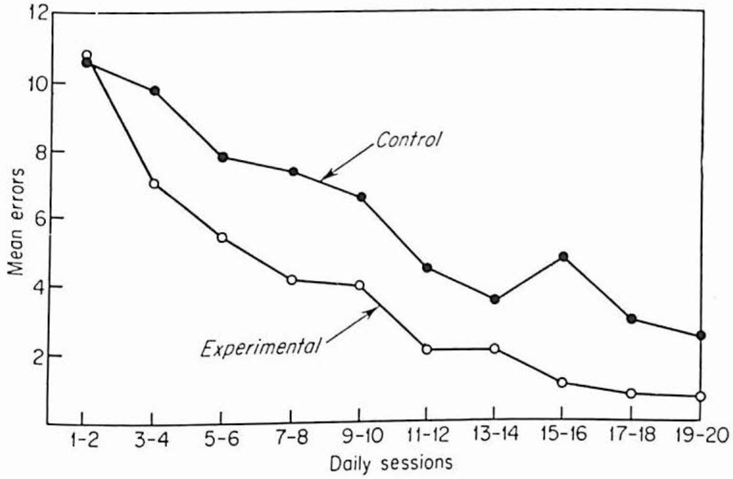

FIG. 10-7. Mean number of errors per two-day block (twenty trials). Both groups receive shock as well as food for the correct choice, but the shock has previously been correlated with food for the experimental group. [*From J. A. Dinsmoor, G. R. Johns, N. D. Kent, W. B. Simon, and Georgia O. Windman, Electric shock as a secondary reinforcer for the correct response in Muenzinger's studies of discrimination learning. Paper read at Midwest. Psychol. Ass., Columbus, Ohio, April,* 1954.]

The transformation of electric shock into a secondary reinforcer has been illustrated in a standard undergraduate laboratory exercise described by Keller and Schoenfeld [28]. Rats were trained to press a bar for food. But each time the food was delivered they also received a mild electric shock through the bar. After the rats were well trained, food was withheld, so that extinction set in. The rate of pressing began to decline. When the extinction had gone far enough, the rats were again given the shock—but no food—each time they pressed the bar. "The result is commonly a rapid acceleration in response rate, which appears as a sizable bump in the cumulative response curve. To an uninformed bystander watching the animal's behavior, it appears that the rats enjoy the shocks and are deliberately punishing themselves" [28, p. 308]. Masserman and Jacques [45] have reported similar findings.

A somewhat different design was adopted by Dinsmoor and his associates [14] in order to analyze some earlier experimental findings. Two groups were given differential pretraining in a runway; both groups received 100 shocks and 100 food rewards, but one group always received the shock and the food on the same trials, while the other group randomly received either, neither, or both on a given trial. For the first group the shock should have become a secondary reinforcer, since it was correlated with the food, but for the second group it should have acquired little or no added significance. Both groups were then tested by training them on a second task, a light-dark discrimination, with shock as well as food for the correct choice. The animals that had shock paired with food on the same trials in the runway showed more rapid learning in the discrimination apparatus and fewer errors. Once again this demonstrates that animals can be trained to "seek" (be reinforced by) a stimulus that is painful or aversive in its original physical characteristics.

SOME FINAL REMARKS

In the first part of this chapter we reviewed the major work that has been done on the problem of experimental neurosis and considered some criticisms of this approach. Later we reviewed a number of attempts to translate more specific clinical concepts into experimental terms and to put them to the test, using animal subjects. The extension of theoretical concepts from one discipline to another is necessarily rather speculative, particularly when the original concepts are poorly defined. Some of the analogies may seem rather strained. Yet this attempt has many values: it forces the formulation of more rigorous definitions in order to subject the postulated relationships to experimental test; it demonstrates the reality of relationships that have often been uncertain; it furnishes new insights with which the clinician may return to his original material. Work with animal subjects has been sufficiently fruitful to have been incorporated on a broad scale in a number of recent theoretical treatments of personality development and psychotherapy.

A related approach, which may prove even more fruitful, reverses the present tack, deriving the initial concepts from general learning and behavior theory based on animal research and testing them on the clinical material. An interesting example of this approach is the recent attempt with psychotic patients to use techniques that were originally developed with the rat and the pigeon. Considerable success has been achieved in training even the catatonic patient to work for hours at a stretch on an indestructible "vending machine" modeled after the bar-pressing box used with rats and the key-pecking apparatus used with pigeons [37]. Direct clinical use of some of these concepts, although less rigorous, may also serve as a helpful test of their fruitfulness in actual practice.

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CHAPTER 11

Genetics and Individual Differences

INDIVIDUAL DIFFERENCES

Variability in the behavior of animals which look alike is apparent to the most casual observer. One shepherd dog stands quietly to be patted by a stranger; another may cringe or attack depending upon the circumstances. If these modes of responding are reasonably consistent from day to day, the first dog may be described as nonemotional, the second as emotional. It is possible to take a large group of dogs and rank them with respect to "emotional" behavior measured by some objective method—the frequency of attacks upon strangers or the amount of heart rate increase when a loud bell is sounded. We are not surprised to find large individual variations in behavior whenever a population of animals or humans is surveyed. People vary in mathematical and linguistic ability; rats differ in maze-learning ability and the tendency to hoard pellets of food.

Investigators have various attitudes towards individual differences. Some, primarily interested in deriving general laws of behavior, find individual variability disconcerting, since it introduces a factor of uncertainty into their predictions. Others orient their research toward individual differences and seek to find the factors responsible for them.

All these factors may be classified under one of two headings: (*a*) genetic factors, i.e., those transmitted from parents to offspring in the sex cells or gametes; (*b*) nongenetic or environmental factors, i.e., those not so transmitted. Note that these are two classes of variables affecting behavior, not two kinds of behavior. Logically, we cannot say that the form of a spider's web is determined solely by heredity. The spider must adjust the shape of his web to the arrangement of available supports. But two different species of spiders will utilize the same supports to produce webs which are sufficiently different to serve as identifying characters. Every response involves an organism with a specific life history and a specific genotype or hereditary makeup. Every response occurs in a situation unique in time and space. We cannot point to any one condition as *the* cause of the response but must recognize that every event is the outcome of a network of causes. The task of psychological genetics is to deal with variations in heredity as they function in this network. Every kind of behavior comes within its scope, and the demonstration that a particular kind of behavior must be learned does not imply that it is uninfluenced by genetic variability.

THE FIELD OF PSYCHOLOGICAL GENETICS

Psychological genetics may be considered as a subdivision of comparative psychology concerned with differences among genetic varieties or strains of a single species rather than differences among species. The limitation to *intraspecific* differences arises from the fact that the basic technique of experimental genetics is the crossing of unlike strains and the observation of the hybrid offspring. Most matings between species are infertile, and their hybrid offspring are almost invariably so. Occasionally there are exceptions to this rule. Clark and his associates [5] studied the inheritance of various components of courtship behavior in hybrids between two distinct though related species of fish.

Research workers in psychological genetics have studied many problems, but all seem to center around one or more of five types of questions.

1. Are individual differences in behavior heritable? This is a basic question, and positive findings must be obtained before proceeding with more searching inquiries. The tendency for certain forms of behavior to "run in families" is evidence for a genetic factor provided all of the families live under identical environmental conditions.

2. What is the nature of the genetic mechanism producing behavioral variation? The answer to this question involves setting up a genetic hypothesis and testing the hypothesis in a breeding experiment. The unit factors of heredity (genes) cannot be directly seen. Thus the testing of hypotheses is statistical rather than observational. Several types of genetic mechanisms are discussed below.

3. How do genes or groups of genes produce effects upon behavior? The connection between a gene in a sex cell and the expression of emotion in a dog is remote. When we have shown that genes do affect emotional expression, we may wish to analyze the effect in terms of body chemistry.

4. How much of the variability found in behavior is caused by differences in heredity; how much by differences in environment? This is the well-known nature-nurture problem which has often assumed importance in human affairs. It is difficult to obtain a clear answer from measurements upon man, because a human family unit ordinarily shares a common environment as well as a common heredity. With experimental animals it is possible to control genetic and environmental factors independently and thus find an answer to the question. More accurately we should

say that we find many answers to the question depending upon circumstances.

5. How does genetic variation within a species affect its social organization, particularly with respect to choice of mates? The survival of a species depends upon the reproductive capacity of its members. If there is psychological discrimination against one genetic variety in selection of mates, that variety may not reproduce in numbers sufficient for survival. Selection in favor of another genotype can lead to an increase in its numbers. Heritable psychological differences have been assigned a major evolutionary role by some biologists.

We shall not attempt to organize the subject to match precisely the order of these questions. Instead, we shall consider some typical experiments in behavioral genetics and return to see what light they throw upon the major problems in the area.

Genes and Traits

A gene is a hypothetical entity based upon overwhelming evidence that heredity has a particulate basis. Genes are to genetics what atoms are to chemistry. The gene hypothesis has been substantiated in many independent ways, and we can be sure that genes are real even though we may never know all their properties. Recently, genes have been described [2] as blocks of complex chemicals known as desoxyribonucleic acid, universally referred to as DNA. All the differences among genes, whether of bacterium, fly, oak, or man, are considered to stem from variations in the arrangement of these blocks. These modifications in the form of a chemical have no essential similarity to the modifications of the traits which they are known to control. Type and color of hair are heritable, but genes are not blond, brunette, or red, nor are they curly or straight. Classifying individuals according to appearance is called *phenotypic* classification. The relationship between genotype (classification in terms of genes) and phenotype is indirect, even for so-called "simple" structural traits. However, the whole of genetical science is based upon the fact that the phenotype of an individual can provide a clue to his genotype.

Current theories [40] emphasize three primary functions of genes: (*a*) reduplication of their own structure, which insures their continuity; (*b*) control of the formation of specific cell components such as the A, B, and O substances in blood cells which determine an individual's blood type; (*c*) the control of specific chemical reactions. The last function seems to be the way through which genes steer the development of an organism.

It is hard to see how these primary functions can result in control of structural patterns such as fingerprints, but the similarity of identical twins proves that they do [24]. Structural and functional differences between individuals *develop*. Only genes are *inherited* in a strict sense. We need words to express the idea that development of a characteristic is modified by genetic differences, without implying that the trait itself is directly transmitted. The terms "heritability" and "heritable" will be used in this sense in this chapter. Both terms are relative rather than absolute. Trait *X* may be highly heritable; the heritability of trait *Y* may be very low.

This is another way of saying that classifying individuals phenotypically with respect to *X* gives a good classification with respect to genotype as well, but that phenotypic classification with respect to *Y* is a poor means of estimating genetic potentialities.

Sometimes a behavioral trait is interpretable as the consequence of a heritable structural variation. Examples are waltzing and circling in mice which result from characteristic lesions in the central nervous system [15]. When organic correlates can be causally related to behavioral variation, the trait is preferably described in morphological or physiological rather than psychological terms. However, no structural basis has been demonstrated for most instances of heritable behavioral variation, either because it has not been looked for in the right places or because it is inaccessible to observation without destroying its identifying characters. Strains of rats have been developed [37] which show reliable differences in maze learning and other psychological tests. At the time of writing there are no clearly established anatomical or chemical differences which can account for this, although the situation may change with advancing knowledge. The proof for the heritability of maze-learning ability does not necessitate showing that this ability depends upon a structural trait which is actually inherited. Instead, the proof depends upon the demonstration that maze-learning ability follows the path of genes as predicted from biological principles. Behavioral measures may well prove to be the most sensitive method of identifying certain genes, just as they are the only method by which we can infer the physiological changes which we call learning.

The use of the term "trait" in psychological genetics needs some clarification. An individual behaves as a whole and is not merely a bundle of traits. As used in the present context a behavioral trait is simply some aspect of behavior which can be reliably measured and is reasonably stable over a period of the life span. This does not mean that genetics cannot deal with developmental characteristics. Rate of change in behavior is a legitimate trait, and many genetic investigations have dealt with variations in learning ability.

An Experiment in Psychological Genetics

Most experiments in psychology involve securing a group of subjects, dividing them into subgroups, treating each subgroup differently, and comparing the results statistically to see whether the treatment has made any difference. Genetic experiments are similar, since producing a difference in genes is one way of giving different treatments. Often, in addition to finding out whether heredity does have an effect, an experimenter wishes to check a particular hypothesis of inheritance. Many of the features of a genetic experiment can be illustrated by a study of audiogenic (sound-induced) -seizure susceptibility in mice which was carried out in the author's laboratory a few years ago [11].

The subjects of the experiment were two inbred strains of mice, DBA/2 and C57BL. Many generations of brother-sister matings (close inbreeding) had reduced genetic variability *within* each strain to a negligible value. One obvious heritable difference was coat color. DBA's are dilute (light) brown; C57BL's are black. DBA's are also highly susceptible to convulsions when exposed at thirty days of age to the sound of a doorbell. C57BL's scarcely ever convulse under the same conditions. Mice of both strains were raised under the same conditions. Since the only systematic difference between DBA's and C57BL's is heredity, this observation by itself supports the hypothesis that seizure susceptibility is heritable.

The particular genetic hypothesis tested in the experiment was: Audiogenic-seizure susceptibility is the result of a single dominant gene. With A symbolizing this gene, the hypothesis can be diagramed:

Strain	DBA	C57BL
Genotypic formula	AA	aa

Genes A and a occupy corresponding positions on the chromosomes (elongated structures in the cell nucleus) and are known as *alleles*. The hypothesis that A is dominant over a means that the phenotype of an Aa mouse will be like that of an AA mouse, not intermediate between AA and aa. The term "phenotype" is here given an extended meaning to include resemblance in behavior as well as appearance.

The experimental test was made by crossing DBA and C57BL mice to produce a first filial generation (F_1). This is shown diagrammatically:

Parental strains	P_1 (DBA)		P_2 (C57BL)
Gametes	A		a
F_1		Aa	

Under this hypothesis, the F_1 hybrids should be as susceptible as their DBA parents. The F_1 generation can be bred among themselves to produce an F_2 and also backcrossed to each of the original parent strains. These crosses and the outcome predicted on the single-dominant-gene hypothesis are shown below. Because of space limitations the diagrams are schematic. If the reader is not familiar with the principles of sex-cell formation and combination, he should consult an elementary biology text which will present the material more completely. For the production of F_2 we have

	F_1 *crossed with* F_1	
Genotypes of parents	*Aa*	*Aa*
Gametes	½*A*, ½*a*	½*A*, ½*a*
Genotypes of offspring	¼*AA*, ½*Aa*, ¼*aa*	
Phenotypes of offspring	¾ susceptible, ¼ resistant	

For the production of the first backcross (Bx_1) we have

	F_1 *crossed with* P_1 (DBA)	
Genotypes of parents	*Aa*	*AA*
Gametes	½*A*, ½*a*	*A*
Genotypes of offspring	½*AA*, ½*Aa*	
Phenotypes of offspring	All susceptible	

and for the production of the second backcross (Bx_2) we have

	F_1 *crossed with* P_2 (C57BL)	
Genotypes of parents	*Aa*	*aa*
Gametes	½*A*, ½*a*	*a*
Genotypes of offspring	½*Aa*, ½*aa*	
Phenotypes of offspring	½ susceptible, ½ resistant	

Table 11-1 gives the observed and predicted values in the actual experiment, when the index of susceptibility was based upon a single trial at thirty days of age.

Table 11-1

Inheritance of Audiogenic Seizure Susceptibility in Mice

Group	Total N	Observed convulse	Observed resist	Calculated convulse	Calculated resist	χ^2
DBA	95	94	1	95	0	
C57BL	50	0	50	0	50	
F_1	73	58	15	73	0	
F_2	112	66	46	84	28	13.41
BX_1	191	175	16	191	0	
BX_2	151	35	116	75.5	75.5	43.7

In the last column are two values for χ^2, a statistic commonly used to test genetic hypotheses. It has been calculated by the formula

$$\chi^2 = \frac{(\text{obs. convulsers} - \text{cal. convulsers})^2}{\text{cal. convulsers}} + \frac{(\text{obs. resistant} - \text{cal. resistant})^2}{\text{cal. resistant}}$$

where Obs. is the observed count of a designated phenotype, and Cal. is the count calculated on the basis of a particular hypothesis. For the second backcross (BX_2) we have

$$\chi^2 = \frac{(35 - 75.5)^2}{75.5} + \frac{(116 - 75.5)^2}{75.5} = 43.7$$

By consulting tables of χ^2 we find this deviation from the expected value highly significant. The hypothesis that susceptibility is caused by a *single* dominant gene must be rejected.

This is the fate of many hypotheses which have tried to explain differences in behavior as being caused by a single gene. Such explanations have been popular, but they should always be regarded with great caution. It is, of course, possible for a chemical or structural modification produced by a single mutation (change in a gene) to have far-reaching effects upon many aspects of behavior. When this is suspected, it is important to identify the chemical variant, show that the trait is inherited, and demonstrate a connection between the chemical and the psychological conditions. This has been done for phenylketonuria, a heritable form of disturbed metabolism in man which produces feeble-mindedness. At this stage of understanding, the problem divides into a physiological-genetics portion dealing with the connection between gene and body chemistry and a physiological-psychology portion concerned with the relationship between chemistry and intelligence. It is no longer a problem in psychological genetics in the strict sense.

QUANTITATIVE INHERITANCE

The methods and concepts employed in the experiment on audiogenic-seizure susceptibility depended upon the fact that each genetic group could be divided into two categories, convulsers and nonconvulsers. Actually, the dividing line was merely a convenience for objective classification. Varying degrees of susceptibility were apparent; with some subjects it appeared to be touch and go as to whether a convulsion occurred, while others convulsed within 10 seconds after sounding the bell. The boundary, though objective, was somewhat arbitrary, and selection of another criterion for susceptibility would have modified the ratios. Nevertheless, a division into two classes does not appear unreasonable and is justifiable on the grounds of convenience and objectivity.

Most behavioral characteristics, however, do not lend themselves to assortment into two or three mutually exclusive categories unless some very arbitrary basis is used to separate the groups. Numbers of errors in a maze, numbers of revolutions in an activity wheel, or numbers of pellets hoarded per unit of time can take any one of a great number of values, and individual variability is expressed in quantitative terms. Most individuals score near the average or mean, and the number of cases falls off more or less regularly on either side. The method of comparing populations with respect to quantitative traits involves determination of the *mean* and *variance* for the trait investigated. Variance, symbolized by σ^2, is the average of the squared deviations from the mean. For example, if the mean of a population is 50, individuals with scores of 52 or 48 contribute 4 units each to variance; those with scores of 45 or 55 contribute 25 units and so on.

Heritability

It is clear that variability in behavior can arise from either hereditary or environmental differences. In an ordinary population of animals breeding in a nonsystematic manner, both kinds of differences coexist. Thus, the total population variance σ_T^2 is the sum of the two variances σ_H^2 and σ_E^2 ascribed to heredity and environment respectively. The total variance can be empirically determined by means of measurements. If there is any way to measure either σ_H^2 or σ_E^2 separately, the other can be found by simple subtraction: $\sigma_H^2 = \sigma_T^2 - \sigma_E^2$.

One way of determining σ_E^2 is to take measurements on individuals selected to be identical in heredity. Differences between such individuals due to genetic variation must be zero and $\sigma_T^2 = \sigma_E^2$. Monozygotic twins are formed by the splitting of a fertilized ovum and share the same complement of genes. In human psychogenetics, comparisons between monozygotic twins and dizygotic twins (produced by separate fertilization of two independent ova) have been frequent. Intrapair differences between dizygotic twins can arise from both environmental and genetic causes. If dizygotic pairs are more unlike than monozygotic pairs in a psychological test, the evidence favors heritability of the trait measured. Monozygotic twins are usually much alike physically (so much so that they are commonly called identical), and the similarities extend to behavior. Part of these similarities may arise from the fact that other people treat identical twins in a more uniform manner than they treat dizygotic twins. Hence, twin data do not give unambiguous answers for the relative effects of nature and nurture, though they have been very useful in studying the heritability of such quantitative traits as intelligence and personality.

With animal material it has been possible to inbreed over many generations so as to produce within strains a genetic uniformity which is close to that of monozygotic twins. The study of such strains and their hybrids has contributed much to our knowledge of quantitative inheritance.

Polygenic Systems

The genetic counterpart of quantitative variation is the polygenic system. In polygenic (or multiple-factor) theory, the strength of a trait is considered to be related to the number of "plus" genes which an individual possesses. In the simplest case, each "plus" gene is equal in effect to every other, and the corresponding "neutral" genes have no phenotypic effect. A population of animals in which plus and neutral genes were distributed according to the laws of chance would show a distribution of genotypes much like the distribution of phenotypes which is commonly observed, a peak at the center and an evenly decreasing number on each side.

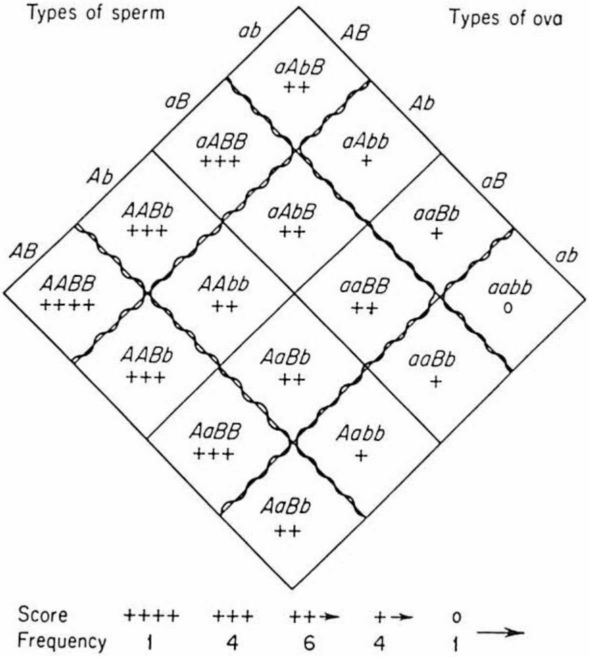

FIG. 11-1. Simplified model of polygenic quantitative inheritance in an F_2 hybrid between two pure breeding strains.

The working of a polygenic system can be illustrated by a simple example. We will start with two inbred mouse strains, one breeding true for two pairs of + genes, *AABB*, and the other breeding true for the neutral or *o* alleles, *aabb*. The phenotype of an individual is considered for simplicity to depend only upon the number of + genes he possesses. The trait affected may be activity, size, average size of litter, or other attributes measured in quantitative units.

If we hybridize these two strains, we obtain an F_1 as shown:

Parents	*AABB* ++++	×	*aabb* *oooo*	Genotypes Phenotypes
F_1		*AaBb* +*o*+*o*		Genotype Phenotype

The phenotype of the F_1 is 2+, which is the average of the parental phenotypes. All members of the F_1 have the same genotype, so that any variability within them must be of environmental origin.

Crossing F_1 individuals between themselves produces an F_2 which is genetically variable. The results can be diagramed as follows: the edges of the grid are labeled with the genetic formulas of the sperm and ova produced by the F_1. The body of the figure contains the symbols for the combinations which are possible, and the numbers of each phenotype are shown below. The average or mean phenotype is 2+, the same as the F_1, but a genetic source of variance has been added. The results in the F_2 group are summarized in Table 11-2.

Table 11-2
Variance in an F_2 Hybrid Population

Phenotype score, x	Frequency, f	fx	Deviation from mean, D	D^2	fD^2
4+	1	4	2	4	4
3+	4	12	1	1	4
2+	6	12	0	0	0
1+	4	4	−1	1	4
0	1	0	−2	4	4
Sum	16	32			16

$$\text{Mean} = \frac{\Sigma fx}{\Sigma f} = 2.0 \qquad \text{Variance} = \frac{\Sigma fD^2}{\Sigma f} = 1.0$$

Polygenic theory can be extended to include systems of many more than two gene pairs and to cover complications resulting from dominance and other interactions between genes. The mathematical treatment can become involved. One important point concerns the best way of measuring a phenotype in order to obtain the most consistent genetic interpretation. This is brought out in the illustrative example.

An Experiment in Quantitative Psychological Genetics

An experiment carried out by Thompson and Fuller demonstrates the application of a polygenic model to a trait labeled "exploratory activity." Mice were placed in an open-ended maze and allowed to explore during six 100-second periods. The total number of sections entered was recorded. Mice of two strains used originally showed vast differences in average activity; Browns entered an average of over 400 sections, while *A* albinos averaged less than 10. In order to facilitate comparisons between such different orders of magnitude, the activity scores were recomputed as the square root of the number of sections entered; 400 sections equal a score of 20, 81 sections equal a score of 9, etc. The results of the experiment in part are shown in Table 11-3.

Table 11-3
Exploratory Activity Scores in C57BR, A/Jax Mice, and Their Hybrids

Type of mouse	N	Mean score	Variance, σ^2
BR	40	22.9	9.74
A	40	1.0°	16.48°
F_1	38	17.0	12.23
F_2	92	16.1	29.60

° Because a large number of A's had zero scores a special statistical adjustment was made in this group, and the values must be considered as tentative.

The F_1 and F_2 hybrids were intermediate in activity to the parental strains, but closer to the more active Browns. This indicates over-all dominance of the "activity" genes. Although the mean activities of the two hybrid generations were not significantly different, the F_2 variance was much greater, as had been predicted, since it included a genetic component not present in the parents or the F_1. If the average of the three upper variances (12.82) is considered a fair estimate of environmental effects, an estimate of genetic variance is: $29.60 - 12.82 = 16.78$. This could be interpreted as meaning that over half the variability in the F_2 generation was from genetic causes. The experiment proves that heredity has a major role in determining the amount of exploratory activity under the conditions of the experiment, but the relative importance of nature and nurture might be quite different in some other test or with different subjects.

PRINCIPLES OF SELECTION

One way of proving that behavior is heritable is to see whether it responds to selection. The starting point for a selection experiment is a heterogeneous population which shows great variability in the character of interest. Some system of scoring is established, and all individuals are tested and scored. Matings are set up between high-scoring males and high-scoring females and usually between low-scoring males and low-scoring females. This procedure can be repeated from generation to generation. It is good practice to maintain simultaneously a random-bred heterogeneous line from the same ancestral stock as a control for the effects of environmental factors, since uniformity of environment is hard to maintain over the long periods of time required to follow several generations. If the random-bred line improves as fast as the selected line, nongenetic factors might be suspected.

Selection for high scores is a method of sorting genes so that a group which tend to elevate scores go into one line, while their alleles which tend to depress scores are discarded. The reverse holds if selection is carried out for low scores. The effectiveness of selection depends upon its intensity and the degree of heritability of the criterion character. Other things being equal, breeding from the upper 10 per cent of the population will produce a "high line" more rapidly than breeding from the upper 50 per cent since plus genes are more concentrated in the upper 10 per cent. Selection is less effective when the criterion character is greatly modified by environment, for a high-scoring animal in such cases may owe his position to favorable experiences which cannot be transmitted to his offspring.

Although the basic principles of selection are simple, complications arise in practice. A common difficulty is loss of fertility in one or more of the selected lines. This may be caused by a disruption of genetic balance in the line through the discarding of genes which contribute to general vigor. Frequently, biologists have found that *heterozygous* individuals (possessing allelic combinations such as *Aa, Bb*) are better adapted than homozygous individuals (*AA, aa, BB, bb*).

Selection for Temperamental Traits

In spite of these and other complications, psychologists and biologists have had considerable success in establishing lines which differ markedly in behavior. A well-known experiment was performed by Rundquist [27] and has been continued by Brody [3, 4]. The criterion for selection was the number of revolutions of an activity wheel over a fifteen-day test period. The averages and standard deviations of "spontaneous-activity" scores for males and females at selected generations are shown in Table 11-4.

Several features should be noted in the table. The activity of both lines was higher in the fourth generation than in the parent stock. Up until this time, selection had been based upon individual records, not upon family records. In other words, a highly active animal from inactive parents might be mated to an active animal from active parents. After the fourth generation, selection was practiced only within lines; high scorers in the inactive line were discarded, and low scorers were eliminated from the active line. The *active* line appears to have lost ground between generations 8 and 12, but this is probably an example of rather large fluctuations from generation to generation which followed no definite order. Females of both lines were more active than their male counterparts because of greatly increased running of females during estrus. The *inactive* strain became extinct at the twenty-fifth generation because of infertility. A new *inactive* strain was subsequently isolated by selection from a group of *active* × *inactive* hybrids. The infertility suggests that selection for inactivity may actually be selection for biologically inadequate rats.

Table 11-4

Selection for Spontaneous Activity in Rats (Rundquist)

(Scores are given in terms of thousands of revolutions per fifteen days. M = mean; σ = standard deviation.)

Sex	Parent stock	Selection line		Generations of selection		
				4	8	12
Male	M = 21	Active	M	143	136	123
			σ	96	70	53
	$\sigma = 10$	Inactive	M	129	15	6
			σ	104	19	5
Female	M = 28	Active	M	181	234	170
			σ	122	70	66
	$\sigma = 22$	Inactive	M	173	39	20
			σ	89	49	24

Selection for "emotionality" and "nonemotionality" was used by Hall [17] to separate two behaviorally distinct strains of rats. The original stock was crossbred from several laboratory colonies. Emotional or timid rats (Hall preferred the second adjective in his later reports) were defined as those which defecated and urinated frequently in a strange situation. The criterion of the emotional nature of this elimination was that it decreased as the subjects became habituated to the test and that defecation scores correlated positively with other indexes of emotional disturbance. The results of eight generations of selection are set forth in Table 11-5. Critical ratios were calculated by dividing the difference between the means of the two groups by the standard deviation of the difference. Values of 2 are generally interpreted as probably significant; critical ratios of 3 or more are highly unlikely to occur by chance. It will be seen that the difference between the two groups was statistically significant after the first generation of selection, but a continued divergence is apparent through the seventh generation. The high values of the standard deviation as compared with the means indicate marked skewness of the distribu-

Table 11-5

Selection for Emotional Elimination in Rats

(Scores for individuals are the number of trials out of 12 in which defecation or urination occurred.)

Generation of selection, P	Mean, 3.86		Standard deviation, 3.54		Critical ratio
	Emot.	Nonemot.	Emot.	Nonemot.	
1	3.07	0.46	3.36	0.77	4.74
2	4.20	1.94	4.12	2.28	2.50
3	3.92	1.02	3.64	1.30	6.00
4	4.69	1.40	3.89	1.43	7.00
5	4.96	0.41	3.85	1.18	8.44
6	6.87	0.51	3.28	1.13	12.72
7	7.82	0.17	3.18	0.47	20.40
8	8.37	1.07	2.94	2.46	14.29

SOURCE: Data from C. S. Hall, Temperament: a survey of animal studies. *Psychol. Bull.*, 1941, **38,** 909–943.

tions. In the later generations most nontimid animals did not eliminate at all, so that the average is a somewhat misleading statistic.

Selection for susceptibility and nonsusceptibility to audiogenic seizures was carried out in mice by Frings and Frings [9]. Starting with a

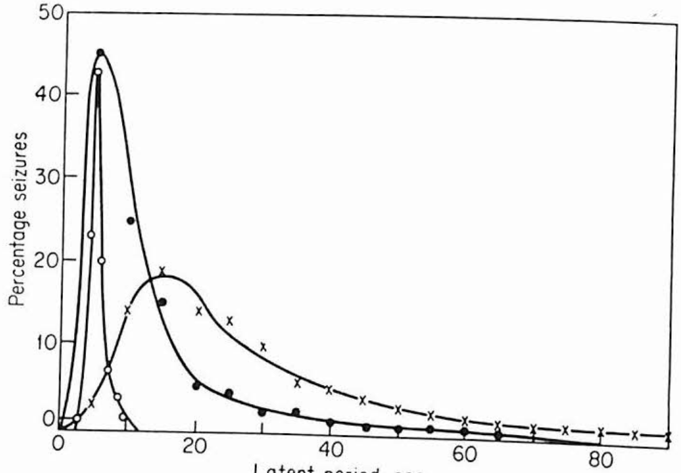

FIG. 11.2. Percentage of total seizures with latent periods shown. (X = original unselected stocks; • = selected for two generations for high seizure incidence; O = selected for seven generations for high-seizure incidence.) The latent periods for the original stocks and second selected generation were read to the nearest 5-second intervals only; those for the seventh generation to the nearest second. [*From H. Frings and M. Frings, The production of stocks of albino mice with predictable susceptibilities to audiogenic seizures. Behaviour*, 1953, **5,** 305–319.]

very heterogeneous stock, these investigators reported the isolation of four strains, each showing peculiarities in the over-all frequency of seizures and in the age of maximum incidence. Figures 11-2 and 11-3 represent the course of selection for high- and low-incidence strains. In both cases a marked effect was apparent after only two generations of selection. Five additional generations of selection in the high-incidence line resulted in a considerable lowering of latencies without affecting the frequency of seizures. In the low-incidence line, further selection produced a slight lowering of average frequency and a definite decrease in the length of the susceptible period. These results suggest that relatively few genes had major effects upon susceptibility, but that a considerable number were concerned with the intensity and duration of the response. During the first few generations of selection the genes with major effect became fixed in the selected lines. The effect of further selection was upon polygenic systems which modified the action of the major genes.

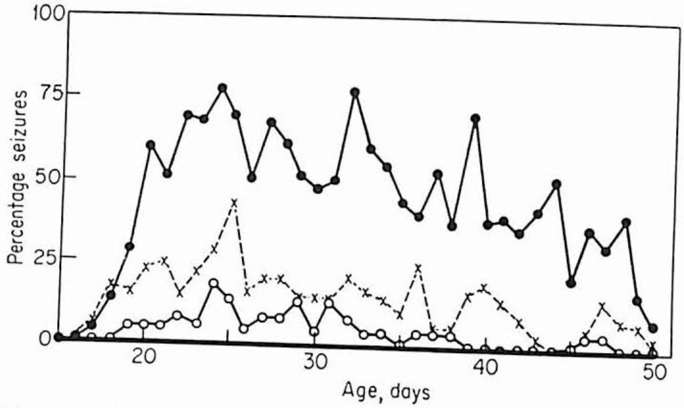

FIG. 11-3. Seizure incidence as a function of age for mice selected for nonsusceptibility to seizures. The solid dark line (at 0 per cent incidence) represents the desired record. (• = record of unselected mice; X = record of mice after selection for two generations; O = record of mice after selection for seven generations.) [*From H. Frings and M. Frings, The production of stocks of albino mice with predictable susceptibilities to audiogenic seizures. Behaviour,* 1953, **5**, 305–319.]

Selection for Intelligence

The selection experiments dealt with thus far have concerned relatively simple modes of behavior. Selection is equally effective when applied to more complex functions such as learning ability. This is well shown by the experiments of Tryon [37] and Thompson [36]. Both of these investigators employed mazes (of different types in the two studies) and produced "bright" lines by breeding rats who made few errors and "dull" lines by breeding their companions who made many errors. Try-

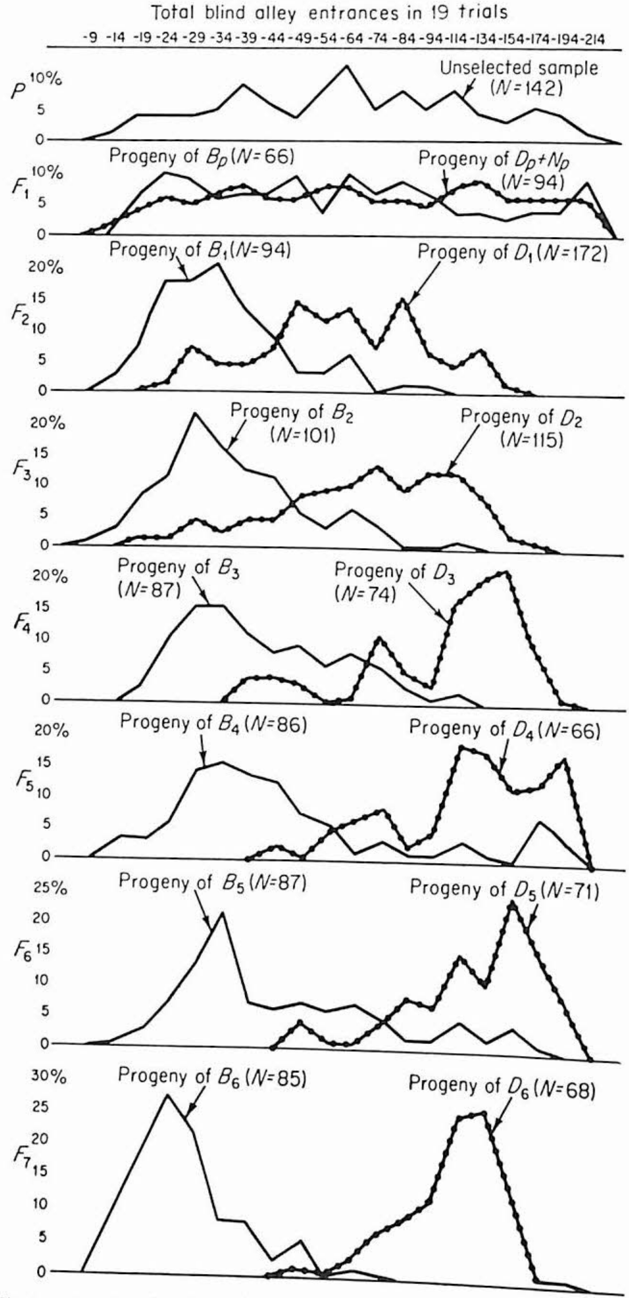

FIG. 11-4. Effects of selective breeding on maze learning. Along the top is the scale of brightness as evidenced by the total number of blind-alley entrances made in nineteen trials. All the distributions below use this common top scale. For instance, a bright animal who made from 10 to 14 errors would fall under the scale step, the upper limit of which is marked −14, a dull who made from 195 to 214 errors would

on's results are shown in Figure 11-4 and Thompson's in Figure 11-5. The terms "brightness" and "dullness" should be used in a restricted sense. The maze-bright animals were not better on all types of learning.

Two lines with predictable differences in behavior may be used as tools to analyze the nature of that behavior. Why does one kind of rat learn a maze more quickly? Is it a matter of sensory acuity, motivation, reasoning, or spatial memory? The answers to such questions can be sought by comparing the performances of the two groups under different conditions and on different tasks. Tryon's contrasting strains have been used in a number of experiments designed to discover the psychological components of maze learning.

Disruption of sensory cues, changing from light to darkness, for example, did not disturb the bright rats, who maintained their superiority. Ratings of emotional responses to two situations: (*a*) when handled, (*b*) when confronted by a novel object in the maze, indicated that bright rats were better adjusted in the maze while dull ones were better adjusted to people. Dull rats performed better in a maze where escape from water was the mode of motivation and seemed less interested in food [31]. This argues for the importance of motivational factors in promoting success. However, bright rats maintained superiority in terms of error scores, whether they were tested after food deprivation or when satiated. The pattern of errors made in the maze was very different for the two strains, indicating that a difference in spatial judgment might be the crucial factor separating them. One worker [20] proposed that bright rats preferred "spatial hypotheses" when presented with a problem which could be equally well solved by using either visual or spatial clues.

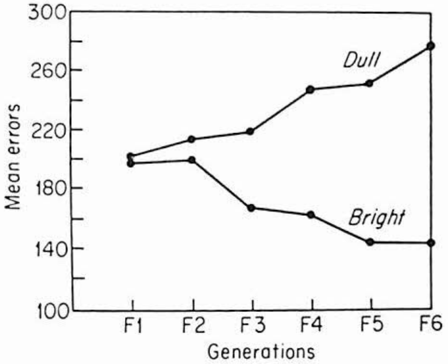

FIG. 11-5. Mean-error scores of "bright" and "dull" rats selectively bred on the Hebb-Williams maze over six filial generations. [*From Thompson*, 36.]

The study of genetically diverse strains has not solved all the problems

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fall under −214, etc. The first generation of rats, marked *P* to the left, is shown just below the scale. The total number of *P* rats was 142, and the per cent of them lying at each point on the scale is indicated in the distribution. The brightest of these were bred together, and then the dullest, giving the two *F* groups, as shown. The selective breeding effects are shown down to the F_7 where progeny of B_6 (bright F_6) are markedly different from the progeny of D_6 (dull F_6). [*From R. C. Tryon, Genetic differences in maze learning in rats. Yearb. Nat. Soc. Stud. Educ.*, 1940, **39**, 111–119.]

of maze learning, but it has been productive of new ideas and led to good experimentation. Selection experiments generally have auxiliary goals, and all the strains mentioned above have been utilized in research programs of diverse kinds.

The conclusion from this array of experiments on selection for behavioral criteria is that positive results have been obtained rather easily when experiments were properly designed. The writer knows of no adequately planned project of this sort which has failed. The conclusion that hereditary differences have widely ramifying effects upon many aspects of behavior is strongly supported, though it should be emphasized that the most highly selected strains are far from uniform in behavior.

The Effects of Single Genes upon Behavior

The results of selection experiments are definite proof that genotypic differences are reflected in behavioral variation. In general, strain differences which appear during selection are attributable to the combined effects of many genes. Is there, then, any basis to the idea that single genes could have major effects upon behavior resulting in simple patterns of inheritance of psychological traits?

The answer to this question is "yes," if we consider as traits the behavioral effects of genes which produce major structural or metabolic anomalies. But what about such common beliefs as, "red-headed persons are quick-tempered"? There seems to be no obvious connection between hair pigment and the physiological traits underlying emotion, but perhaps this is merely a reflection of incomplete knowledge of metabolism. This type of problem has been studied experimentally in animals.

Coat color has been hypothesized to correlate with temperament in animals, and a great deal of anecdotal material of this type has been compiled [19]. Because a particular color gene is associated with an aggressive strain of rats does not mean that color has any necessary relationship to temperament. The strain has to have some color, and the particular association may be an accidental product of selection. To determine whether a single gene has effects upon behavior not predictable from its major metabolic effects requires that animals be produced which differ genetically at only one gene position. Technically, this is difficult to accomplish with certainty, but an approach can be made. Experiments on phototaxis (going toward light) [29] and rate of wing beating [39] in Drosophila have shown that single eye-color genes do modify behavior which appears unrelated to the conspicuous effects of the genes.

Possibly every gene substitution could potentially influence some type of behavior, but ordinarily the effects are swamped by the interplay of uncontrolled genetic and environmental variation.

THE GENETICS OF RACE AND STRAIN DIFFERENCES

Most species can be divided into more or less distinct subpopulations which are variably known as races, breeds, and strains. Such groups are defined as collections of individuals sharing the same gene pool. Genetic differences among races, human and nonhuman, have been frequently investigated. All such studies tend to the same conclusion: genetic differences among races are quantitative rather than qualitative.

Two general kinds of explanation have been proposed for the origin of racial differentiation. The first considers selection as a sort of sieve with different-shaped openings in different environments. Races of the rock-pocket mouse in the Southwest tend to match the soil color of their own habitat. Presumably, mice which blend into their background are less likely to be caught by predators, and more likely to leave descendants. Selection tends toward different end points in regions where soils are distinctively colored [8].

Artificial selection has been practiced by man in his development of breeds of domestic animals. Unlike natural selection, the end point of artificial selection is generally usefulness for man rather than adaptability of the animal. Often the process is directed against biologically useful behavior patterns. Selection for high egg production in fowl involves discarding genetic factors favoring broodiness, for a poultry man cannot afford to give his flock a vacation from egg laying in order to carry out their maternal functions. In nature a nonbroody fowl could not survive, but she is favored in a world where giant automatic devices serve *in loco parentis* to myriads of baby chicks.

A second cause of racial differentiation is *genetic drift*. As its name implies, this phenomenon involves chance, nondirectional changes in gene frequency. Suppose, for example, that ten different psychology laboratories each obtained one pair of rats from a large, genetically heterogeneous colony. Each pair could hand down to its progeny only those genes which it possessed at the time of separation from the large colony, and the particular assortment would be different for each pair. In each colony over a number of generations some genes might be lost, some added by mutation or outcrossing. In a few generations each group would be distinctive, and none exactly like the parent colony from which all were derived.

An effect somewhat like genetic drift but more rapid is produced by inbreeding a number of lines from a heterogeneous population. After a few generations of brother-sister matings, each line tends to become homozygous for all or most of its genes. An inbred line is comparable to an individual whose genetic constitution can be reduplicated over and over again. Geneticists have limited control, however, over the nature of the genotype which is fixed, since the particular gene assemblage fixed is a matter of chance.

Racial and Strain Differences in Behavior

Some of the most interesting comparisons between strains have involved the wild Norway rat and his cultured relative, the laboratory rat. Wild rats seldom reproduce in the laboratory. They are aggressive toward handlers and difficult to manage even when reared from infancy. Selection can be credited with making the domestic rat into a useful experimental animal. In selecting for docility, however, various other physiological and behavioral characteristics have been carried along which may limit the general application of results gained from experiments on this most popular animal of experimental psychologists.

For example, after castration an ordinary white rat from laboratory stock runs much less in an activity wheel. This has been interpreted as evidence for a stimulatory effect of sex hormones upon activity. However, castrated *wild* rats are no less active than intact animals [26]. Wild rats seem to be less dependent upon their gonadal hormones. In contrast, they are more affected by removal of their adrenal glands, a procedure which is tolerated by domestic rats provided adequate salt is supplied in the diet [25]. Domestication has involved selection for a different hormone-behavior relationship. This possibility must always be held in mind in generalizing results from one variety to another.

The list of reported differences in behavior between strains is fairly extensive. A few findings will be mentioned as examples of the range of phenomena investigated. C57BL mice show more emotional elimination (Hall's test) than do BALB/c mice [10, 23]. A series of 15 mouse strains tested for exploratory activity showed a 23-fold difference between the highest and lowest average scores [35]. Rats from a black-hooded stock hoarded more pellets than either a brown-hooded or an Irish stock. In addition, hoarding behavior was elicited much sooner in black-hooded rats when they were placed in a favorable situation [33].

Female rabbits of race *X* build nests earlier on the average than do race-III females [28]. Snowy tree crickets exist in two races which appear identical but can be separated on the basis of their song and habits of oviposition [13].

Perhaps the most important feature of the laboratory data is the common occurrence of behavioral differences in the absence of previous conscious selection. The biologists who originated these laboratory stocks were not concerned with differences in emotionality, hoarding, or amount of activity. A degree of psychological distinctness seems to be an almost inevitable concomitant of biological differentiation.

Most studies of strain differences have concentrated upon a single character. Recently a large-scale investigation of the role of genetics and behavior was undertaken in which multiple measurements were made on each individual [30]. Dogs of five breeds were the subjects, and two of these, African basenjis and cocker spaniels, were crossed in order to study the genetic mechanisms concerned with transmitting behavior traits. In practically every test, evidence was found that heredity had some influence upon performance [12]. Some results are summarized in Table 11-6.

Table 11-6

Comparison of Dog Breeds on Several Behavior Tests

Nature of test	Nature of score	Average score of breed samples [*]				Significance of differences
		Basenji	Beagle	Spaniel	Terriers	
Cue response: going to signal for food reward	Percentage of correct trials	74	88	77	84	0.01
Learning to walk on leash in prescribed manner	Number of demerits	56	39	32	27	0.001
Spatial orientation: finding food on an elevated maze	Number of errors	169	131	105	179	0.001
Motivation test	Time in seconds to run to food	4.9	2.7	3.0	2.7	0.01
Autonomic expression of emotionality	Heart rate change when person approaches	+15.0		−5.2	+7.5	0.001
Aggressiveness to handler	Arbitrary rating scale	18.5	19.9	14.3	21.4	
Intralitter dominance	Percentage of clear dominance-subordination pair relationships	68	28	42	91	0.01

[*] Each breed was represented by the descendants of one or two pairs. Because of the restricted range of sampling, no conclusions should be drawn regarding the nature of the breeds as a whole. The breeds were simply used as sources for samples which were expected to be more different than samples drawn from a genetically homogeneous population.

The rank of the breeds varies from test to test, indicating that a particular genotype in dogs facilitates specialized kinds of learning but not learning in general, or specialized expression of emotionality, not emotionality as a unit trait. Intercorrelations between test scores tend to be low except when the tests are very similar. The evidence favors the hypothesis that heritable individual differences in animal behavior are specific for particular kinds of behavior.

Inheritance of Behavior in Interstrain Crosses

Crosses between strains varying in behavior have often been made. Table 11-7 summarizes a few experiments which illustrate a variety of

Table 11-7
Results of Hybridizing Strains of Unlike Behavior

Behavior measure	Species	Cross	Results	Reference
Rate of running in activity wheel	Rat	Active by inactive selected strains	F_1 active but less so than active parent. Genes for activity generally dominant in other crosses.	[3]
Running speed	Mouse	Wild by tame (fast versus slow)	F_1 slightly less fast than wild parent. F_2 and backcross data agrees with polygenic inheritance. Genes for speed generally dominant.	[7]
Errors in maze	Rat	Bright by dull selected strains	F_1 intermediate to parents. F_2 similar and about as variable as F_1.	[37]
Number of pellets hoarded	Rat	Brown-hooded by Irish (high by low hoarders)	F_1 has a high hoarding score similar to B-H parent. Backcross to B-H is intermediate, possibly a bimodal distribution.	[34]
Errors in "spatial orientation"	Dog	Basenji (many errors) by spaniel (few errors)	F_1, F_2, and backcrosses make equal or fewer errors than spaniels.	Fuller and Scott (unpublished manuscript)
Docility test	Dog	Basenji (low) by spaniel (high docility)	Reciprocal F_1s differ. Young resemble mother. Hybrids intermediate but tend to be like mother.	Fuller and Scott (unpublished manuscript)

outcomes. Sometimes the F_1 is intermediate to its parents. This may be interpreted as due to additive gene action. Other experimenters have found the F_1 closer to one of the parental stocks and have cited this as evidence for partial dominance. Sometimes the F_1 falls outside the parental range (row 5 of the table). Such results may be interpreted as indications of complex trait interactions. Possibly several biological characteristics are inherited in an additive manner, and a combination of intermediate-strength traits may have the greatest psychological efficiency. This could lead to hybrid vigor in adaptive behavior.

PATHWAYS BETWEEN GENES AND BEHAVIORS

Genes are biochemical entities and operate directly as components of biochemical systems. More complex characteristics which are "inherited" must be dependent upon transactions between biochemical systems and the whole assemblage of physical, biological, and psychological factors which are lumped together as "environment." As we have emphasized above, it is not necessary to understand the details of all these transactions in order to establish the heritability of a trait. The inheritance of maze-learning ability in rats has been well established by breeding tests and the results of selection, in the absence of any conclusive data relating learning ability to biochemical factors. Similar statements could be made about the inheritance of many physical traits, such as color patterns or body conformation. Such characteristics are the end points of a series of developmental processes which are incompletely understood.

Nevertheless, a complete account of the relationship between genetics and behavior must deal with the way in which genes produce their effects. The general procedure is to start with heritable differences in behavior, and attempt to relate these to a heritable anatomical or chemical trait. An example of this approach may be cited from human genetics [18]. A sizable group of feeble-minded children show no gross brain defects which might explain their lower intelligence. Some of these undifferentiated mental defectives have been found to eliminate abnormal amounts of phenylketone and related substances in their urine. Phenylketone is an intermediate product in the oxidation of phenylalanine, one of the amino acids, which are the units from which proteins are built. The failure of an enzyme to catalyze its oxidation has far-reaching consequences on behavior. The defect is inherited as a simple recessive. However, the discovery of an inherited biochemical deficiency is not the end of the problem. How the metabolic deficit produces its psychological effect remains to be learned. Two possibilities are (*a*) the end product of the reaction is essential to mental development, and the blockade prevents the synthesis of an essential substance; (*b*) the substances (phenylketone, for example) which accumulate behind the blockade are toxic and interfere with behavioral development.

The kind of therapy which might be effective in overcoming the effects of the gene would be very different in the two cases. In one situation, an attempt would be made to supply the missing end product. In the other, effort would be directed towards neutralizing the toxic material or eliminating from the diet the raw material, phenylalanine. The latter procedure has been reported to give favorable results.

Among the explanations for genetic effects upon behavior are: enzyme deficiencies resulting in partial or complete metabolic blocks; variations in hormone production or in sensitivity to hormones; variations in the number, size, or arrangement of brain cells; and variations in the strength of simple reflexes, the acuity of sense organs, or the excitability of particular neural centers. These ideas are not mutually exclusive but reflect differences in methods of study which may be biochemical, electrophysiological, anatomical, and so forth.

Biochemical Variations and Behavior

A general impairment in the metabolism of the nervous system could have far-reaching effects upon behavior [14]. There are almost numberless possibilities for genetic variation in enzyme systems, and the effects of any variation might depend upon concurrent variations in related enzymes. There is some evidence that the strain differences in audiogenic-seizure susceptibility which have been found in mice are dependent upon an underlying variation in an enzyme system concerned with the supply of energy to brain cells [1]. Susceptibility is associated with a low concentration of the enzyme adenosinetriphosphatase in the brain. Concentration of the enzyme in the susceptible DBA strain increases with age, and there is a correlated increase in resistance to audiogenic convulsions.

Other researchers have reported a correlation between problem solving behavior in rats and the concentration in the brain of another enzyme, cholinesterase [21]. This enzyme catalyzes the breakdown of acetylcholine, one of the "chemical transmitters" concerned with the passage of nerve impulses between nerve cells. It is likely that the investigation of enzymes and brain function will become increasingly important. Since genes are so directly connected with enzymes, all findings in the area have potential significance for psychological genetics.

Endocrine Glands, Heredity, and Behavior

The pituitary, thyroid, adrenal, and sex glands are well-known organs of the endocrine system. Their products, known as hormones, are secreted into the blood and affect metabolism in many ways. Hormonal effects on behavior also have been known for many years, and variations in endocrine physiology have been proposed as causes of individuality. Differences in hormone output, if determined genetically, are one path through which genes might operate to produce behavioral variation. A second possibility is genetic modification of the response to hormones. These alternatives have been tested in a recent series of experiments [16, 38].

Sex behavior in the male guinea pig is dependent upon a supply of hormones normally produced in the testes. After castration, sexual responses to a female in heat rapidly decrease and practically disappear. In these investigations considerable variation in strength of sexual activity was found among intact males. Those from an outbred, genetically heterogeneous stock were much more active than were males from two inbred strains. Behavior was quantified in two ways: on a scale based upon the intensity of activity in successive time samples during a test period with a receptive female and on the basis of counting specific items of behavior, such as attempted copulations. After individual differences had been reliably established by a series of tests, subjects were castrated. Sex-behavior scores fell rapidly but were restored when adequate doses of testosterone were injected. Provided the amount of artificially administered hormone was large enough, there was no relationship between dosage and sex-behavior scores. The level of activity attained by each injected castrate was correlated with his precastration score. Previously low-scoring animals remained low, even when they received the same quantity of testosterone which restored high-level activity to the previous high scorers. This experiment demonstrates that differential responsivity to hormones is the critical factor in producing sex-behavior variation in male guinea pigs.

Another general type of question concerns the relation between physiological and psychological effects of hormones. Cortisone, from the adrenal cortex, is known to be a powerful physiological agent, and it has also been reported to have behavioral effects (including the production of psychoses in humans undergoing cortisone therapy). Various strains of inbred mice are known to differ in their physiological sensitivity to injected cortisone (measured by changes in the white blood cells), and experiments have been conducted to see whether physiologically sensitive strains also show greater behavioral response to this hormone [10]. The answer appears to be negative. Quantitative differences in the behavior of two strains, selected to be physiologically distinct with respect to their cortisone response, were singularly resistant to large doses of injected cortisone as well as to removal of the adrenal glands. The adrenal cortex is considered important in the organism's response to stress. Experimental procedures applied to the mice included electric shock, and the hormone injections themselves would seem to have been "psychologically stressful." The experiment yielded no evidence that genetic variation in response to psychological stress was mediated through the endocrine system. Behavior differences between the strains were not changed by adding to or subtracting from the supply of adrenal hormones.

Although much research has been conducted on hormonal effects upon behavior, few researchers have simultaneously manipulated the genetic variable. The experiments cited suggest that variations in hormone production may be relatively unimportant as causes of behavioral variability within the normal range. However, the nature of the substrate upon which hormones operate has a major role in determining their behavior effects. This is illustrated by the comparisons between wild and domestic rats previously cited [25] as well as by the experiments described in this section.

Neural Variation and Genetics

Studies on hereditary variation in the nervous system have been almost completely restricted to the effects of single genes which produce major anatomical deficiencies. A large number of genetic anomalies have been described in man, mice, and other mammals. Behavioral consequences of neurological deficits vary according to the region affected. Blindness, deafness, and disequilibrium are frequently found to have an hereditary foundation. Hyperactivity, circus movements, twitching and jerking are other common results of particular genes. Deficiencies of intelligence commonly accompany major neurological deficits in man. The psychological attributes of circling, waltzing, and shaking in mice have not been thoroughly studied, though Yerkes published an important contribution to the field in 1907 [41].

Circling behavior in mice is not always the result of a single-gene-produced deficit. Strains can be selected for little or much running in circles, and the amount of circling depends partly upon the environment [6]. Presumably this behavior results from some neurological condition.

Variation in quantitative characteristics of the central nervous system is as great or greater than in other body systems [22]. Possibly the pattern of arrangement of nerve cells and the density of cells in the different layers of the brain is a characteristic of each individual just as are his fingerprints. But even if this proves true, we have no inkling of how the variations in the finer anatomy of the nervous system are related to behavior, and the technical difficulties involved in finding out are almost insurmountable. Genetic control of development is, in fact, about the only way in which such anatomical variation might be brought under experimental control.

To sum up, the pathways between genes and behavioral variation are best understood in those cases in which major anatomical and metabolic deficits are involved. The kind of quantitative behavioral variation within the normal range which responds to selection and which is characteristic of differences between strains has rarely been correlated with organic factors. In part, this reflects the difficulties inherent in the problem, and in part, the lack of a concerted research effort directed to finding such correlations.

PSYCHOLOGICAL FACTORS AND EVOLUTION

The genes of an individual influence his behavior, but the reverse is not true. Once a genotype is determined, it remains the same irrespective of the pains and pleasures, the learning and forgetting which are the fate of its associated phenotype. In the long run, however, behavior does affect the composition of the gene pool and may thus be thought of as a force in evolution. Animals whose behavior is maladaptive are likely to die without leaving descendants; hence, their genes are lost to subsequent gene pools. This process, operating through millennia, has been responsible for a remarkable coordination of behavior patterns and specific environmental niches. The relationship of behavior to evolution was recognized by Darwin who devoted a chapter in *The Origin of Species* to this subject.

Heritable variation in courtship and mating behavior is particularly important in this respect since it is so intimately related to reproduction and the transmission of genes. Some species which will mate in captivity and produce hybrids fail to do so in nature. The inference is that psychological rather than biological incompatibility is the isolating factor. Many studies on the fruit fly Drosophila have demonstrated preferential mating between males and females of a particular subspecies [32].

Selective mating over a period of generations can produce important effects upon the distribution of genes. Some biologists have speculated that psychological isolation is an important evolutionary factor in those species capable of making fine discriminations.

SUMMARY

On page 326 it was stated that most research in psychological genetics is concerned with one or more of five fundamental questions. Statements may now be made regarding each of these:

1. Individual differences in many aspects of behavior have been shown to be heritable. In fact, psychological variation seems to be a concomitant of biological variation although there is no one-to-one correspondence between biological and psychological traits.

2. Many single genes producing structural variations (usually defects) induce behavioral traits related to the structural defect. Much behavioral variation seems to depend upon polygenic systems, although the simplest genetic models do not exactly fit the observed facts. Often one set of alleles ("activity genes," for example) is dominant over alleles with opposite effects ("inactivity genes"). At other times the strength of a trait appears to be related to the sum of plus and minus alleles which are present.

3. Except for genes producing conspicuous physical or chemical defects, little is known of the way in which hereditary effects upon behavior are related to the primary biochemical action of genes. Perhaps the balance between a large number of independently controlled processes is more important than the level of any one process.

4. The proportion of individual psychological differences ascribable to genetic factors is not constant but varies according to the population considered and the condition under which it is observed. Determining the heritability of a trait in quantitative terms is valid only when all factors are specified. It is possible to demonstrate that heredity is quite important, or that it is unimportant, for one and the same trait. A full investigation of nature-nurture relationships requires a broad base of experiments with all pertinent factors varied systematically.

5. Genetic effects upon individual behavior can modify group behavior. Such effects may have evolutionary significance if they lead to selective mating and increased propagation of certain genotypes.

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CHAPTER 12

Behavior and the Nervous System

THE "BRAIN-BEHAVIOR" PROBLEM

What is the relationship between the structure and function of the nervous system and the organization of behavior? The question is an old one. The "brain-behavior" problem has traditionally been a subject of interest to comparative psychologists, physiologists, and anatomists. The solution of the problem is proving difficult because a valid neuropsychology requires the independent identification of both the behavioral and the nervous system events under study. Historically, the work in this area has been hampered by a failure on the part of investigators to concern themselves with the independent definition of events and by a lack of necessary research techniques. As a result, the specification of the relationships between behavioral and neural events has not progressed as rapidly as might be hoped. Nevertheless, a consideration of psychological and biological research techniques and findings is a point of departure for evaluating the contribution of the comparative method to this field of psychology.

The *comparative anatomist* studies the changes in nervous system structure that accompany evolutionary development. This work has given us much of our present knowledge of the developmental principles of neuroanatomy and the structural interrelationships of its components. The *neurophysiologist* has used the comparative approach to help define such structure-function relationships as the excitation and conduction of impulses within the neuron and the process of synaptic transmission. The *comparative psychologist* has made some progress in deriving basic behavioral principles coordinate with these fundamental biological principles. The chapters in this book show his contributions to the formulation of ontogenetic and phylogenetic principles of behavioral development. On the whole, however, advances in this area have come rather slowly. The formulation of valid neuropsychological principles requires the detailed analysis of the properties of an organism's behavior. Only such an analysis will yield the precise definition of behavioral events required for the formulation of the necessary principles.* Few comparative investigations have been aimed at the derivation of such principles. This may be one consequence of the psychologist's traditional concern with vague "faculties" and "functions," an approach which does not suggest the type of analysis from which the required neuropsychological principles can be formulated.

In this chapter we shall first direct our attention to established evolutionary and maturational principles of development. Then we shall turn to a consideration of those methods which characterize the development of research interest in this area. Finally, we shall describe some of the contributions of comparative research to our understanding of the role of the nervous system in such areas as sensory processes, motor patterns, motivational activities, innate patterns, learning, and emotion. In so far as possible, we shall confine our treatment of the "psychological" phenomena in these areas to those aspects of the organism-environment interaction which can be operationally defined. The more traditional approach to the brain-behavior problem has emphasized the role of brain structures as "seats" or "centers" for somewhat elusive "functions" or "capacities." This approach often leads to the erroneous implication that a psychological event is "explained" when a nervous system correlate has been uncovered. In reality, the best we can hope for is a specification of the nature of neural participation in any given segment of behavior. In keeping with this attitude, an attempt will be made to emphasize the *relationships* between independently defined behavioral and neural events that have been uncovered by comparative study.

THE NERVOUS SYSTEM AND BEHAVIORAL DEVELOPMENT

Differentiation and Centralization

The phylogenetic and ontogenetic development of biological forms generally conform to a broad principle of *differentiation* and *centralization*. As we ascend the phylogenetic scale, we find that the nervous system progressively differentiates into more and more specialized tissues and that the organization of these tissues changes from a diffuse system to one in which ganglia (clusters of nerve-cell bodies) develop and become centralized, integrative structures. The operation of this general principle may be seen in the maturation of the individual as well as in the evolution of organisms. Similarly, we find that the organization of behavior also follows this general principle.

Invertebrates. In its first and most primitive form, for example, the

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* This concern for greater precision in our definitions of behavior is not unique to neuropsychology. The reader is referred to the chapter on abnormal behavior (Chap. 10) for a fuller discussion of this problem.

nervous system appears as a diffuse, undifferentiated, and noncentralized network, or plexus, of nerve cells whose branching fibrils run throughout the organism (Fig. 12-1*a*). There are no centers of integration, and the net serves only for conduction. There is little opportunity for the differential reinforcement and inhibition of neural activity. Stimulation of sensory cells results in transmission throughout the entire organism. The

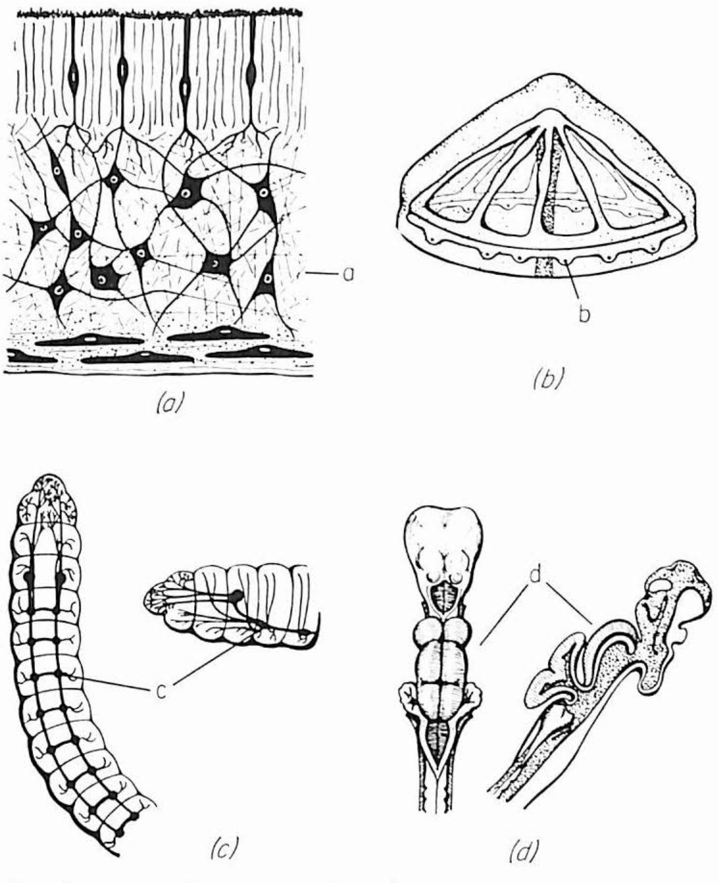

FIG. 12-1. Semidiagrammatic representation of nervous system development in phylogeny. Primitive coral forms (*a*) characteristically show the diffuse nerve net illustrated by the region marked *a* and consisting of undifferentiated ganglion cells and branching fibrils. In the jellyfish (*b*), the nerve plexus begins to mass at certain points and forms the nerve ring illustrated by the region marked *b*, consisting of a ringlike duct with a nerve cord. The earthworm (*c*) typifies the early appearance in many invertebrate insect forms of a centralized organ system with differentiated segmental ganglia, as illustrated by the region marked *c*. And in the characteristically vertebrate nervous system of the dogfish (*d*), the ganglionic or synaptic components congregate to form a central mass, as illustrated by the region marked *d*, and the development of longitudinal fiber systems serves to integrate the activity of widely separated segmental and suprasegmental structures.

behavior of primitive coral forms, which are typical of this level of neural development, is similarly diffuse and is limited to an undifferentiated response to a relatively narrow range of environmental stimuli. The characteristic reaction of such animals to intense stimuli is a contraction of the whole organism.

In the next highest stage of neural development, found in some jellyfish forms, the process of differentiation and centralization first begins to appear (Fig. 12-1*b*). The nerve plexus forms a mass at certain points and becomes distinct from other parts of the system. The nerve net has become a nerve ring (the first definite localization of neural elements), and now the effects of all stimulation must be transmitted to one general area en route to the effectors. We have here the beginnings of a centralized nervous system which contrasts to the peripheral plexus illustrated in Figure 12-1*a*. Even with this structure, behavior continues as a restricted, somewhat diffuse responsiveness to a limited number of stimuli. Only small gains in the differentiation of responses are apparent. For example, the jellyfish *gonionemus* swims slowly by rhythmic pulsations of its bell. At times it exhibits a fishing technique in which it swims to the surface, turns over, and floats slowly down with tentacles outstretched to trap its food. This free-swimming response of the jellyfish requires a more elaborate neural mechanism than the nerve nets of the sedentary coral or the very slow-moving anemone [12].

The spiny-skinned animals, the *echinodermata*, such as the starfish, are usually classified just below the invertebrate chordates since in their early stages of development they show the bilateral symmetry characteristic of fast-moving animals. As an adult, the starfish shows a radial symmetry not unlike that of the jellyfish. Its nervous system is only an elaboration on the nerve ring mentioned earlier. It consists of a ring encircling the mouth which gives off a radial nerve into each of the five arms. Differential sensitivity is somewhat greater with this arrangement and, when suddenly exposed to a strong stimulus or when righting itself, the starfish will show some variability and flexibility of behavior. For the most part, however, the activity of the starfish is primarily reflexive and highly stereotyped.

A most significant development in nervous system evolution is seen in higher invertebrate forms. Here a centralized organ system with differentiated segmental components makes its appearance. In the worm, for example, separate structures exist which provide for sensory, motor, and ganglionic (synaptic) relationships at each body level (Fig. 12-1*c*). This ladderlike organization permits a considerable increase in local-behavioral efficiency, which is illustrated by the capacity of the earthworm to acquire a simple neuromuscular habit such as learning a maze [32].

On the whole, the behavior of the invertebrates is not very flexible or adaptable, however, and we have indicated that their nervous systems are concentrated into not one but several differentially located masses. The limited behavioral repertoire of these organisms is related to this lack of a real central unity in their nervous system organization.

Vertebrates. The vertebrate nervous system is characterized by a much greater degree of structural and functional unity than that found in the invertebrates. While some of the segmental features of the structure of the worm are retained, the ganglionic or synaptic components congregate to form a central mass. Longitudinal fiber systems develop which serve to integrate the activities of widely separated segmental or suprasegmental components (Fig. 12-1*d*). This centralized structure with its many interconnections and its specialized systems permits the neural impulse to be combined and directed in many ways. Herein lies the great advance of the vertebrate nervous system over that of the invertebrates—an advance that would appear to have important implications for neural-behavioral relationships.

Rostral Development. Many striking and important modifications take place in the nervous system as we ascend from *amphioxus* * to man. Of these, perhaps the most important in terms of their implications for behavior are the developments at the rostral or head end of the organism. This is not to imply that a teleological principle is operating here. We do not say that rostral development took place "in order for" the animal to survive but only that the development of rostral organs resulted in better conditions for survival and adaptation. In general, the evolutionary process has resulted in structural arrangements allowing for the intake of food at the rostral end. In the case of forward-moving animals, environmental stimuli are first encountered by these rostral portions, and it is not surprising to find special sensory and motor developments appearing around this primary input source. For example, phylogenetic developments have progressively altered the location of receptors for smell sensations from their wide distribution over the entire body, as in some aquatic forms, to such confined areas as the nasal cavities of mammals. Vibration sensitivity, too, appears to be widely distributed in the lateral-line organs of some lower species, but only the single rostrally-located pair of ears survives in the higher forms. And, of course, visual receptors appear at the location which is best suited for observing what the moving organism is approaching. Thus, important sense organs are seen to develop at the rostral end of an animal in accordance with a body plan which seems to provide the most satisfactory conditions for survival and adaptation.

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* A marine animal typical of the *notochords* which possesses some structural characteristics that appear to provide a link between the intervetebrates and the vertebrates. These features include a *notochord*, a cartilagelike rod which extends the length of the body and supports the soft tissue, the dorsal tubular nerve cord, and the pharyngeal gill slits.

On the motor side, too, phylogeny features extensive rostral development. The development of an oral cavity, jaw muscles, and even taste sensitivity is related to the intake of food. Oxygen intake is more readily accomplished through rostrally placed organs since the forward motion of the organism can actually be seen to produce currents through the oral and nasal cavities. In the fish, the gills, just caudal to the head and supported by a structure called the branchial arch, serve to expel the inspired water, while more advanced mammalian forms develop vocal organs in close association with this respiratory apparatus. Extensive changes occur in the more primitive branchial arches in the process of the development of these functions. The more advanced forms eventually even become capable of complex facial expressions. Finally, special musculature required for such functions as eyelid closure, eyeball movement, and pinna adjustment develops in this same head region. These refinements function either to protect the rostral sense organs or to make them more efficient in their operation.

It is difficult to overemphasize the importance of these great sensory and motor systems in the evolution of behavior. They provide the organism with a highly refined sensitivity to and control over the most complex aspects of the outer world. This vast and variable external environment appears to demand a more flexible behavior than the automatic regulation which seems to be adequate for dealing with the organism's inner visceral world. Special refinements are necessary for coordinating a multitude of sensory inputs and motor responses. The elaboration of extensive nervous system interconnections in the vicinity of the head clearly reflects this need.

Encephalization

Neurobiotaxis is a theory sometimes used to account for the apparent movement of nerve cells toward their point of stimulation. This theory runs into difficulties when applied to specific cases [28], but it has some general explanatory value. Neurobiotaxis is assumed to play a major role in the emergence of specialized sensory and motor nuclei from the primitive reticular substance in the rostral portions of the neural tube. Through the migration of nerve cells toward their point of stimulation, fiber tracts are formed which permit coordinated interaction between the several sensory and motor systems. Next comes the development of suprasegmental structures with their intricate vascular supply and accessory supporting tissues, and we find that the brain or encephalon has become a dominant reality. These higher structures are connected to the sensory and motor nuclei of the lower centers by long fiber tracts and by relay systems which extend the entire length of the neuraxis (brain and spinal cord). As evolution continues, the development of the brain is characterized by ever-increasing growth, complexity, and control over the lower centers. This principle is called *encephalization.*

Phylogeny. The nature of the relationship between the neural development that we have been discussing and the evolution of behavior may be illustrated by the comparative literature on nervous system ablations. These studies investigate the effect of the experimental destruction of neural tissue on behavior at various phylogenetic levels. In general, limitations in the organism's ability to interact with environmental stimuli as a result of damage to higher nervous centers appear to be much more severe in the higher vertebrates than in the lower. In the absence of the cerebrum, for example, the fish and the bird show no detectable disturbance of motility. The rat, cat, and dog demonstrate impaired posture but can stand and walk; the monkey can sit with help but is unable to walk. Finally, human beings without the cortex are capable of neither posture nor locomotion. Essentially the same relationship is also apparent in the visual behavior of organisms without the cortex. The fish shows no impairment after removal of the visual cortex (occipital neocortex, Fig. 12-2); the bird has some disturbance of detail vision; the rat cannot discriminate visual patterns but can distinguish the brightness, position, and

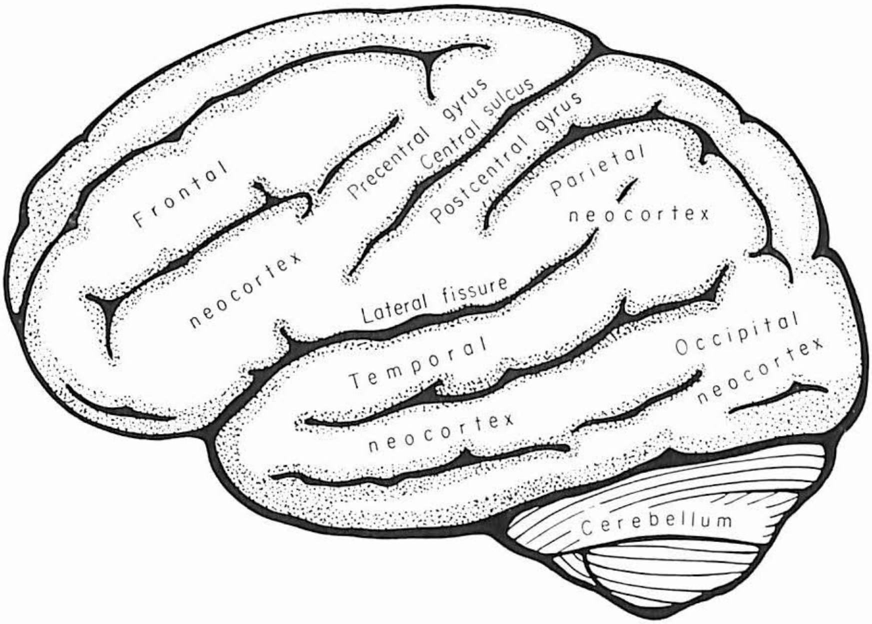

FIG. 12-2. Semidiagrammatic representation of the lateral surface of the human brain.

distance of objects. The cat, dog, and monkey can react only to brightness, and man is completely blind [18]. Even some of the more broadly defined "learning" phenomena appear to follow this same general course in vertebrate forms after decortication. Unfortunately, the specification of the behavior variables in these studies often leaves much to be desired. For example, it may be difficult to decide whether an impairment of performance in a manipulative task following the destruction of cortical tissue really results in a loss of ability to "learn" or "remember" or is simply due to a loss of dexterity. With a lack of more precise definitions of these psychological phenomena, it becomes hard to specify their relationship to nervous system structure and function.

Ontogeny. In the maturation of the individual organism the relationship between nervous system and behavioral development appears to be even more striking. Ontogenetically, the first gross undifferentiated responses give way to discrete and relatively specific fetal reactions to local stimulation. This change in behavior corresponds to the development of segmental arcs prior to their unification or centralization. In fact, the intricate adaptive-behavior patterns of late fetal and postnatal life may be interpreted as an organization of these early, specific responses to stimulation. As maturation progresses, the development of the more complex adjustive processes becomes increasingly dependent upon the refined sensory and motor functions of rostrally-placed end organs. The organization of behavior clearly reflects this unified, centralized, and integrated control by a progressively encephalized nervous system.

The development of the plantar reflex serves to illustrate this intimate relationship between stimulus-response events and neural maturation. In the human, the mature plantar reflex consists of a downward (ventral) contraction of all the toes to local stimulation of the sole of the foot. The earliest response to a relatively discrete stimulus to the sole of the foot is a local muscle twitch occurring only at the point of stimulation. At the next level of development there is an upward (dorsal) movement of the toes to this local stimulation—the Babinski reflex. This corresponds temporally to a limited intersegmental development of spinal cord connections. As encephalization proceeds to the integration of the midbrain and spinal cord, the response changes to include a ventral extension of the great toe. The other toes continue to move dorsally in response to the stimulus. Finally, the development of forebrain dominance corresponds temporally to the emergence of the mature plantar reflex, and all the toes contract ventrally. This relationship between changes in simple behavioral events and the development of the nervous system provides a reliable indicator of neurological damage. The appearance of the Babinski reflex in later life is taken as an indicant of organic disorders involving the long motor systems of the mature neuraxis.

Summary

Clearly, then, the general pattern is discernible in both phylogeny and ontogeny. The diversity, richness, and complexity of behavior increase in close temporal correspondence to the progressive centralization and encephalization of the nervous system. Adaptability to variable and complex environmental conditions develops through the integration and elaboration of responses originally made to more uniform and simple situations. This increasing plasticity or docility of behavioral patterns is contiguous with the increasing flexibility of the nervous system. As centralization or unification progresses, the organism is provided with an infinitely variable response repertoire. Indeed, this general evolutionary and maturational pattern seems to be reflected in the tendency of the organism to adapt the environment to its own use, in contrast to the more primitive adaptation of the organism to its environment. The developmental theme thus centers around an increasing complexity of both behavior and the nervous system. The temporal correspondence between their phylogenetic and ontogenetic courses provides a reasonable basis for believing that the comparative approach is valuable in the definition of neuropsychological relationships.

METHODS FOR THE ANALYSIS OF BRAIN-BEHAVIOR RELATIONSHIPS

Techniques

A variety of physiological and psychological techniques have been applied to the problem of identifying and defining the characteristics of neural participation in behavioral events.

Microscopic Analysis. This technique is used to investigate the structural connections between peripheral receptors and effectors and specific, centrally-located neural masses (nuclei). Gross structures may be sectioned, stained, and examined to trace neural pathways. The definition of specific anatomical relationships which this technique provides gives us the first link in the relational chain between behavior and the nervous system. For example, the limits within which the behaving organism can receive environmental stimuli are set by the structures of the primary sensory systems for vision, audition, olfaction, and so forth. Likewise, the structural relationships within the motor systems determine the nature and extent of the responses the organism can make in interacting with the environment. While microscopic analysis has been helpful in uncovering these anatomical relationships, the determination of functional relationships between anatomical factors and behavior has had to depend upon somewhat less direct research methods.

Artificial Stimulation of the Nervous System. This has proven to be a useful experimental tool for such functional analyses. With this technique, attempts are made to excite specific neural components, usually by electrical or chemical means, and the consequent motor effect is recorded. The use of artificial stimulation in comparative studies has provided information from a variety of experimental animals about the functional relationships between the nervous system and at least some of the more basic sensorimotor events which constitute behavioral building blocks. Some studies with humans have employed this method. The patient undergoing brain surgery is often given only a local anesthetic which enables him to remain conscious during the operation. Verbal reports of the sensory experiences related to the stimulation of specific regions can be obtained from these individuals [25].

Electrical Recording. The minute electrical potentials associated with the activity of the nervous system can be picked up by electrodes placed on the surface of or implanted within nervous tissue. With proper amplification, these potentials may be recorded to give an indicant of changes in neural activity resulting from both artificial and natural stimulation, e.g., sound and light. This association between nervous tissue activity and changes in electrical potential has provided a basis for extensive work with electroencephalographic (brain-wave) recordings from the surface of the skull. Attempts to define specific brain-behavior relationships with such electrical recording techniques have occupied a prominent place in the neuropsychological literature for the past two decades [14].

Ablation. Probably the most popular comparative approach to the problem of brain-behavior relationships is that of experimental *ablation* techniques. Portions of the nervous system may be destroyed by either surgical or electrolytic methods and changes in behavior following the selective production of these neural deficits investigated. This technique has been used with many animal species, including man. With laboratory animals, such efforts usually involve four steps: Some specific form of preoperative training or, in some cases, careful observation of normal behavior; ablation; the evaluation of postoperative behavioral changes, if any; and finally, the post-mortem verification of the extent and location of the damage by histological means.

The use of this method with the neurosurgical patient or the traumatically brain-injured human presents several problems. Through illness or accident such people usually become subjects in these investigations quite unexpectedly, and careful observations of preoperative behavior are seldom available. As a result, the systematic information needed to define the behavioral side of the investigation is usually lacking. Furthermore, postoperative assessment often depends upon either tenuous comparisons with group performance norms or subjective estimates of change.

Finally, accurate histological information is difficult to obtain for obvious reasons.

Usually, two or more of these methods are used in combination with one another. For example, an electrode may be implanted in the cortex of a rat, the region may be stimulated, and observations made of motor responses. When this phase of the experiment is concluded, a strong "coagulating" current may be passed through the electrode to destroy the nervous tissue in which it is embedded. The animal is then sacrificed, the brain removed, stained, and examined microscopically to determine the size and extent of the area affected. This makes it possible not only to localize the lesions made but also enables the histologist to trace the structure of the system involved. By studying the degeneration of fibers in sections taken from more remote areas of the neuraxis, he can sometimes determine the structural relationships between neural components involved in the response. The development of new staining techniques which make it possible for the histologist to see unmyelinated as well as myelinated fibers promises to increase the effectiveness of this method.

Interpretation

Both clinical studies with their obvious difficulties and the more rigorous experimental studies with infrahuman species involve similar interpretative problems. Inferences concerning normal brain-behavior relationships which are based only upon data obtained from the injured organism must be accepted with extreme caution. Furthermore, considerable refinements in the definition of behavioral events presumed to be related to specific portions of the nervous system are required before reliable neuropsychological principles can be established. The physiological and anatomical techniques we have been discussing will be of maximum value only when the elements and functions of a given behavioral event are rigorously specified.

Despite the many problems involved, the broad outlines of at least some basic neural-behavioral relationships are discernible in the research reports concerned with sensory processes, motor patterns, motivational factors, learned behavior, emotional patterns, etc. Comparative methodology has played a prominent role in furthering our understanding in these areas.

SENSORY PROCESSES

The central nervous system correlates of sensory phenomena have been explored in a wide variety of animal species. Careful comparative neuroanatomical, neurophysiological, and behavioral studies have established the foundations of an extensive neuropsychology in this area. The experimental analysis of neural participation in cutaneous, olfactory, and gustatory sensitivity has depended heavily upon direct anatomical observation, stimulation methods, and electrical-recording techniques. Ablation studies have played a role in these analyses, too, although the destruction methods have been applied most extensively in studying the neural-behavioral relationships associated with vision and audition.

Touch, Pain, and Temperature

Much of the exploration of the neural structures associated with touch, pain, and temperature has been based on the neuroanatomical and electrophysiological analysis of specific spinal cord, brain stem, and forebrain systems. (The reader may refer to any standard textbook in physiological psychology, e.g. Morgan and Stellar [19], for a description of these systems, which include the lateral and ventral spinothalamic tracts, the trigeminal nerve and its nuclei, the nucleus gracilis and nucleus cuneatus, the ventral posterior and arcuate nucleus of the thalamus, and the postcentral gyrus of the cerebral cortex.)

The role of these neural components in somesthetic events has been explored at several phylogenetic levels, including man. For example, in one procedure used, the skin is stimulated and changes in electrical potential are recorded from points on the postcentral gyrus. The electrocortigrams thus obtained from the monkey, chimpanzee, rabbit, and cat [31] reveal an orderly representation of somesthetic sensitivity in this area. In the monkey and chimpanzee, this representation, in the sequence of leg, arm, and face (within these areas still more restricted parts are present in orderly sequence), proceeds ventrally over the dorsal and lateral surface of the postcentral gyrus. While the rabbit and cat lack a true postcentral gyrus, this representation, in the same general sequence, is found in an area corresponding to the postcentral gyrus of the primates. In humans the verbal responses of conscious neurosurgical patients to direct stimulation of the cortex reveal the same orderly representation of peripheral somesthetic sensitivity [23].

The sensory cortex does not appear to be essential for the simple experiencing of touch, pain, and temperature. Responses to these stimuli appear mediated by the thalamus (Fig. 12-3, p. 375) and are little disturbed by removal of the sensory cortex. Comparative studies, however, suggest an interesting phylogenetic relationship between the sensory areas of the cortex and behavior requiring more complex discriminative reactions. Experiments in weight discrimination, summarized elsewhere [19], appear to indicate that loss of sensory cortex affects this performance least in the monkey, more in the chimpanzee, and most in the human, who cannot make such discriminations at all. Once again it appears that the principle of encephalization is operating. As we ascend the phylogenetic scale, the structural and functional integrity of the "higher" neural components becomes more and more essential for behavior.

Olfaction and Gustation

The olfactory and gustatory systems have received only a limited degree of interdisciplinary attention with respect to brain-behavior relationships. Nonetheless, both neuroanatomical and electrophysiological observations have suggested the participation of specific forebrain structures in behavior resulting from the excitation of these sensory modalities. For example, structural and functional relationships between olfactory sensitivity and specific portions of the limbic system (basal and lateral amygdaloid nucleus, septal region; Fig. 12-3) have been found. There is a lack of behavioral data in this area, however, and a more detailed neuropsychological analysis will have to wait for further investigation. The use of methods for determining taste thresholds for quinine in animals, combined with ablation techniques, reveal an association between specific thalamic nuclei (ventral posterior) and gustatory sensitivity. In the monkey, experimental lesions in the thalamus have resulted in higher thresholds for preferred solutions, indicating a lowered taste sensitivity [22]. The involvement of relatively specific cortical areas in gustatory events has also been suggested. Clinical studies of persons with gunshot wounds show that a relationship exists between disturbances of the lateral surface of the frontoparietal lobe (posterior and ventral to the central sulcus but dorsal to the lateral fissure, Fig. 12-2) and verbal reports of alterations in taste sensitivity [4].

Vision and Audition

The prominence of hearing and seeing in organismic-environmental interactions has produced a most extensive analysis of nervous system participation in these processes. The structural and functional relationships between the brain stem and forebrain components of these primary sensory systems have been analyzed from primitive animal forms to man. The course of the auditory impulse over the VIIIth cranial nerve, through various specific neural centers (cochlear nucleus, superior olive, inferior colliculus, and medial geniculate body) to the temporal neocortex (Fig. 12-2), has been analyzed in comparative studies using electrical recording techniques. The visual system has also undergone extensive electrophysiological investigation. Specific neural structures (lateral geniculate body, superior colliculus) intervening between the retina and occipital neocortex (Fig. 12-2) have been identified and their functional and structural interrelationships analyzed.

Behaviorally, however, more extensive analysis seems indicated before the relationships between these specialized neural components and organismic-environmental interactions can be properly defined. While some significant contributions to this area have come from clinical observations of human patients, the major source of our neuropsychological data has been comparative studies on a variety of animal species. In these studies, animals are typically conditioned to visual or auditory stimuli, ablations made, and changes in performance observed. Restricted lesions in the specific neural centers involved in audition have been made in laboratory animals (principally the cat). These are related to decrements in learned food-getting and avoidance responses conditioned to the pitch, intensity, or localization of auditory stimuli [13], although the precise nature of these relationships is as yet unclear. Similarly, performance deficits in learned-response patterns involving visual stimuli such as form and brightness have been related to lesions restricted to specific areas of the occipital neocortex [16]. Here again, however, further investigation is needed before the precise nature of the participation of specific visual components in such behavioral events can be specified.

Despite these difficulties, comparative studies with these and other sensory modalities appear to confirm the principle of encephalization. In general, damage to "higher" nervous system components produces greater behavioral deficits at the more advanced phylogenetic levels.

MOTOR PATTERNS

Both ontogenetic and phylogenetic studies have played a role in the investigation of motor patterns. Early studies tended to focus on the close temporal correspondence between the appearance of relatively specific muscular-response patterns and the maturation of various nervous system components. Somewhat more direct observations have been made possible by the development of electrophysiological stimulation and recording techniques. These methods, used with a variety of animal species, indicate an even more precise role for specific neural structures in the organization and elaboration of specific motor responses.

Spinal and Lower Brain Stem Reflexes

In its most basic form, the nature of this relationship is reflected in the monosynaptic segmental arc as represented by the *myotactic* reflex. This reflex, a component in limb flexion and extension reactions, consists of a contraction of a muscle following sudden stretching. It is based upon the simplest affector-effector structure: Impulses entering a given segment of the spinal cord, via a sensory neuron, synapse directly on motor neurons of the same segment. In this case, activity in specific motor neurons is found to be associated with discrete muscular responses. The comparative approach has also been used in the investigation of the more complex intersegmental and suprasegmental reflexes (i.e., postural reflexes). Studies of supporting, shifting, and righting behaviors in carnivores such as the cat and dog have given us some insight into the role of specifically organized brain stem (vestibular nuclei), cerebellar, and cortical participation in fundamental motor-response patterns. In the shifting reflex, for example, a shift of body weight onto a flexed limb results in a strong extensor tonus in the flexed limb. This facilitates the support of the shifted weight. The response appears to be organized in the lower centers of the brain. It is well defined in the midbrain animal, present but less well organized in the animal with suprasegmental structures above the medulla removed, and absent in the spinal animal [19].

Cortical Involvement

Studies with monkeys and human infants, using ablation and electrophysiological techniques, have indicated that portions of the precentral gyrus of the cerebral cortex (Fig. 12-2) are related to the grasping reflex [26]. Indeed, the specific representation of localizable peripheral movements on the dorsal and lateral surface of the precentral motor regions has been well documented in both man and several infrahuman mammals. Direct electrical stimulation of the dorsal surface of this cortical region, for example, produces toe and foot movements. Correspondingly, specific response patterns involving the knee, hip, trunk, hand, arm, neck, and face can be elicited as discrete stimulation proceeds ventrally over the lateral surface of this area.

The more complex aspects of motor coordination and integration are also critically related to central nervous system structure and function. Animal experiments in this area have been hampered by difficulties in defining and controlling the behavioral-response patterns under investigation and in specifying their relationships to specific neural events. In general, however, experimental and clinical observations of brain-injured organisms have confirmed the relatively specific involvement of both precentral neocortical and neocerebellar structures in the maintenance of coordinated postural and manipulative movements and in motor facilitation and restraint. Ablation studies with rats, cats, dogs, and several varieties of primates as well as extensive observations on brain-injured humans by clinical neurologists all point to such relationships. The phylogenetic development of dependence upon these more "advanced" neural structures for coordinated motor patterns has been well documented.

MOTIVATIONAL ACTIVITIES

The role of the central nervous system in behavioral events associated with the satisfaction of such basic needs as sleep, general activity, and hunger has been the subject of several comparative studies.

Sleep

For example, ablations performed on monkeys and rats indicate that fairly well-defined areas of the hypothalamus (Fig. 12-3) may be involved in sleep and wakefulness patterns. Lesions in the more lateral and posterior portions of this structure (mammillary bodies) have produced abnormally prolonged periods of "drowsiness" or profound sleep [24]. Ablation of more anterior hypothalamic regions (preoptic nuclei) appears to result in sleeplessness [20]. Similar disturbances in sleep-wakefulness cycles have been reported in human patients with growths and inflammations of the hypothalamic areas. More recently, portions of the midbrain reticular formation also have been found to play a role in sleep functions. This finding comes from studies with carnivores and primates which have employed ablation, stimulation, and recording techniques.

Activity

The problem of determining neural participation in general-activity-levels has been investigated in several animal species. Studies with rodents, carnivores, and primates suggest that both cortical and subcortical structures are involved in general-activity changes. Ablation in both cats and monkeys indicates that damage to striatal portions of the forebrain (caudate nucleus, among others) produces measurable alterations in activity-levels. Portions of the hypothalamus (ventromedial nucleus) also appear to be involved, at least in the rat. Unfortunately, the precise character of such experimentally produced changes in activity is not clear. In large part this is due to difficulties with the experimental definitions of activity-level. Because our operational definitions of behavior are provided by the techniques and the apparatus that we use, further attention needs to be given to the refinement of our present methods of measuring activity. Behaviorally, only the most general indications of increases or decreases in drum-rotation frequencies or stabilimeter movements are usually reported. This leaves us without precise measures of behaviors which casual observation would seem to insist should be included in a definition of general-activity-level. Furthermore, these measures usually do not tell us whether changes are in amount of activity or in the character of activity. It is possible that a reduction in locomotor activity observed in an activity wheel might be related to an increase in restless activity which the wheel does not record. Probably the most reliable neural-behavioral relationship in this area involves the hyperactivity which has followed ablation of the frontal cortex (Fig. 12-2) in nearly all species studied (rat, cat, monkey) [19]. Considerable effort has been directed toward defining the specific groups of cells within the frontal region that are associated with this effect. In addition, recent observations of clinical patients with neurological and psychiatric disorders promise to shed considerable light on neural events involved in general activity.

Hunger

Unfortunately, little is known about the role of the nervous system in motivational activities associated with such fundamental bodily needs as evacuation and thirst. Few, if any, systematic comparative studies have been devoted to these topics. The neural correlates of hunger have been investigated more extensively, and comparative studies have made a significant contribution. For example, direct electrical stimulation of the central nervous system tissue of several animal species indicates that differential changes in gastric motility can be related to specific portions of the hypothalamus. Stimulation in the medial region increases stomach contractions, while stimulation of the posterior hypothalamus inhibits this response (Fig. 12-3). The relationship of eating behavior to neural components has been explored using destruction methods. A variety of animals has been used, although the most extensive work has been done on the rat. Dramatic increases in food intake (hyperphagia) have been observed to follow lesions of the ventromedial nucleus of the hypothalamus, while lesions somewhat more laterally placed in this same region appear to inhibit eating behavior [8]. Other stimulation and ablation studies indicate that portions of the frontal neocortex also may be directly related to the regulation of food intake. The precise character of these interactions has yet to be determined.

INNATE BEHAVIOR PATTERNS

A number of relatively complex behavior patterns have been conventionally regarded as being predominantly innately organized. For the most part, migration, hoarding, hibernation, mating, nest building, and maternal behavior are thought to be heavily dependent upon specific neural structure-function relationships. With the possible exception of sexual behavior, however, there appears to be a relative dearth of systematic studies aimed at defining the precise character of such behavior patterns.

Hoarding and Maternal Behavior

Ablation studies with rats have implicated the more medial aspects of the cerebral cortex in hoarding behavior, and it now appears that lesions in the area of the cingulate cortex (Fig. 12-3) are related to a reduction in hoarding [29]. In general, however, the facts about this behavior have not been well integrated, and it has been suggested that investigations be extended to include such "natural" hoarders as hamsters, squirrels, and mice [27]. Lesions in the rat have indicated that damage to more than 20 per cent of the cortex seriously impairs such maternal activities as nest building, retrieving, nursing, and protection of the young [3]. Recent work suggests that, as in the case of hoarding, disruption of these behaviors is related to damage in the cingulate (and retrosplenial) areas of the cortex. Destruction of the dorsolateral cortical surface apparently has no effect [30].

Sexual Behavior

The most extensive neuropsychological inquiries in this area have been studies of the participant role of nervous system components in various aspects of mating behavior. For example, comparative studies with amphibia and mammals have convincingly demonstrated that a well-organized sexual response depends upon specific inputs from the primary sensory systems. These studies, summarized elsewhere [2], demonstrate that interference with vision, olfaction, and audition can seriously impair mating behavior.

In addition, there are the results of physiological studies involving several animal species such as the rat, guinea pig, cat, dog, and human patients with only the spinal cord intact [2]. These studies indicate that at least some of the reflex aspects of the total sexual pattern may be organized primarily in the spinal portions of the central nervous system. Many of these same species have been decerebrated at different levels. Apparently the further integration of sexual behavior which is related to estrual response to hormones depends to some extent upon components of the posterior hypothalamus and anterior midbrain. In addition, localized lesions of the ventral hypothalamus, between the optic chiasma and the stalk of the pituitary (Fig. 12-3), in rats and guinea pigs have been reported to impair or abolish mating behavior [10].

Perhaps the most significant contributions of comparative-psychological studies in this area, however, have come from the analysis of cortical participation in various aspects of sexual activity. For example, studies with decorticate female infraprimates such as the rat, rabbit, cat, and dog have shown that the cortex is not essential for the arousal and satisfactory execution of the mating pattern. It does play some role in the refinement of the pattern, however, and is also related to the extent to which the female will take an active part in initiating sexual activity. With male animals, on the other hand, comparative decortication studies have revealed a different picture. In rodents, the degree of sexual impairment appears to be positively correlated with the extent of cortical damage. The detrimental effect of such lesions on male animals higher on the phylogenetic scale has been even more pronounced. The completely decorticate cat, for instance, is indifferent to a female in heat and will not mate even when placed in the proper position [2].

Thus, the analysis of the relationships between sexual behavior and the nervous system once again reveals the operation of the neuropsychological principles of progressive encephalization [1].

LEARNED BEHAVIOR

Many of the neuropsychological aspects of learning appear to be inseparable from the study of sensory processes, motor patterns, and motivation. In addition, however, an extensive comparative literature is devoted to the specification of the role of the nervous system in conditioning, "habit" formation, "problem solving," and so forth. For the most part, ablation techniques have been the most widely used, and the neuropsychological emphasis has been on the cerebral cortex. More recently, studies involving the direct electrical stimulation of deep-lying subcortical structures have provided another approach to the investigation of learning situations. The pioneers in this field were Franz and Lashley, who used extirpation methods and maze learning [17]. These classic experiments, begun more than four decades ago, represent the first systematic comparative approach to the analysis of nervous system participation in learning. Since that time, many comparative studies utilizing a wide range of animal species have explored the effects of selective neural damage upon the acquisition, retention, and extinction of both simple and complex discriminative learning.

Conditioning

In general, these studies indicate that some learned behavior does not necessarily depend upon the integrity and organization of the cerebral cortex. In the rodent, carnivore, and primate species used, the simple conditioning of salivation, eye blink, avoidance, and other such responses occurs despite large lesions in the cortex. Even completely decorticated preparations have been trained to give adaptive anticipatory responses to stimuli involving any one of several sense modalities. The dog can give a conditioned paw withdrawal in response to tactile, auditory, visual, and thermal stimuli in the absence of cortical tissue. It can even learn to discriminate between two stimuli, responding to a light but not to a sound [9]. The precise role of the brain stem and spinal cord systems in mediating such "conditioned" responses is still far from clear.

"Problem Solving"

The participation of relatively discrete neural components is apparent in learning situations involving conventional "problem solving" behavior.

For example, maze-learning experiments of the type mentioned earlier indicate that the rat's acquisition and retention scores can be related to the extirpation of cortical tissue: the more complex the maze and the more extensive the lesion, the greater the behavioral deficit. For the most part, however, these studies have not been able to specify the particular cortical regions participating in the learning process. Only in some of the more recent investigations, involving delayed responses in primates with cortical lesions largely restricted to the prefrontal areas, has some light been shed on this aspect of the problem. Following such selective neural damage, hungry monkeys show marked performance decrements when forced to delay only a few seconds before choosing, from a pair of cups, the one under which they have seen food placed. Extensive lesions in other cortical areas appear to have no effect on this behavior [15]. It would seem likely that considerably more numerous and subtle relationships among specific nervous system components and various aspects of learned behavior will become apparent as we ascend the phylogenetic scale. However, the definition of the characteristics of such interactions must await future comparative analysis. Recent advances in electrical-stimulation and electrical-recording techniques, as well as in methods for biochemical analysis, promise to provide a more direct approach to the analysis of neural events which play a role in the learning process.

EMOTIONAL BEHAVIOR

In many respects it seems hardly justifiable to consider emotional behavior independently of the innate and learned aspects of neuropsychology. Nevertheless, many comparative efforts to uncover neural-behavioral relationships have focused upon a class of behavioral events from which qualitatively different affective states are inferred. Here again, a variety of animal species has been studied and extensive use has been made of the ablation and stimulation techniques. In the analysis of emotional behavior and its neural correlates, subcortical structures have commanded the most attention. As early as 1888, for example, changes were reported in the emotional behavior of rhesus monkeys following deep lesions which involved the amygdala and other subcortical structures (Fig. 12-3) [11]. Numerous studies over the past fifty years or more have continued the attempts to unravel neural-behavioral relationships in this area.

For the most part, studies with a wide variety of animal species (rodents, carnivores, primates, and even man) have implicated a group of functionally related forebrain structures in the mediation of many such affective processes. The components of this group, most recently referred to as the "limbic" system, are still not very well agreed upon but generally include the hippocampus, pyriform lobe, cingulate gyrus, septal region, amygdala, thalamus, and hypothalamus (Fig. 12-3). Early studies with decorticate preparations (primarily cats and dogs) revealed that many basic aspects of rage and fighting behavior, for example, appeared in the absence of most neocortical tissue but with critical limbic-system components intact. More specifically, selective changes in behavior patterns conventionally regarded as "emotional" ("rage," "fear," "pleasure") follow both the stimulation and the ablation of specific hypothalamic nuclei (i.e., ventromedial nucleus), the septal region, amygdala, and other limbic structures. Similar effects have failed to appear in studies directed at other portions of the nervous system [6].

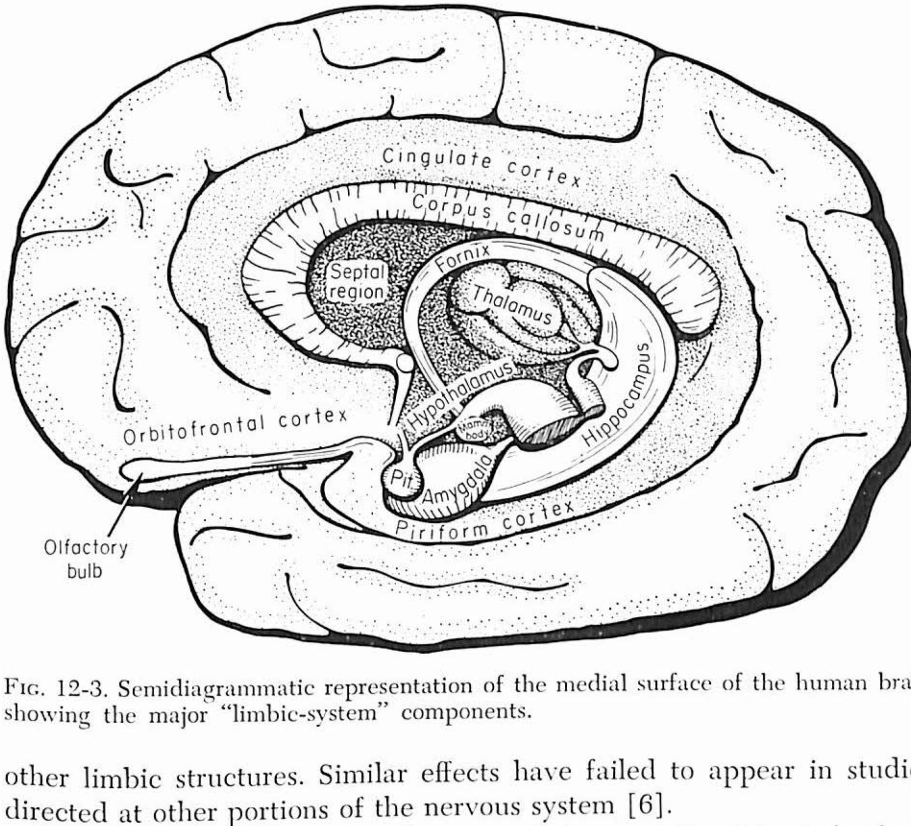

FIG. 12-3. Semidiagrammatic representation of the medial surface of the human brain showing the major "limbic-system" components.

Needless to say, the precise character of these relationships is far from clear. This is largely due to the difficulty of defining, either experimentally or clinically, those distinguishable properties which are to provide the behavioral basis for delineating "emotional" changes. More recently, however, improvements in behavioral control methods have made possible more refined operational definitions of emotional-response patterns and of specific relationships within the nervous system. For example, a conditioned emotional response of the "fear" or "anxiety" type may be defined as a suppression in the rate of bar pressing for food caused by the introduction of a noise which has previously been associated with shock. Experiments using such dependent variables have begun to show the relationship between specific neural components and these carefully defined, if somewhat atomistic, aspects of emotional behavior.

Lesions in the septal area, hippocampus, and portions of the hypothalamus have been found to weaken such a conditioned emotional response. Extensive damage to the higher neocortical structures appears to leave the "fear" behavior relatively unaffected [7]. In addition, electrodes have been chronically implanted in these deep-lying structures of the limbic system. Recent studies with rats, cats, and monkeys have shown that direct electric stimulation of many of these areas can be rewarding to the animal. When the situation is arranged so that lever pressing produces stimulation, the animal will maintain a high rate of responding for long periods of time [21]. Furthermore, conditioned "fear" responses, established in lever-pressing situations using liquid or food rewards, fail to appear when the animals are pressing the bar to produce brain stimulation in certain of these limbic structures [5]. Certainly, some most exciting prospects appear to be emerging from the comparative psychology laboratory with respect to the elucidation of central nervous system participation in affective behavior.

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CHAPTER 13

Theoretical Foundations of Comparative Psychology

INTRODUCTION

The study of comparative anatomy by the premedical student prepares the way for his grasp of human anatomy in much the same manner as the study of comparative theory by the beginning psychology student prepares him for the complexities of human psychological theory. It was no accident that theories now applied on the human level were first developed in the studies of infrahuman species. On the one hand the basic assumption was that behavior of all organisms followed the same fundamental laws, and on the other the complexities of human behavior made it difficult for the observer or theorist to see some of the basic processes involved in man's activities. As has been shown in preceding chapters, these considerations justified the attempt to discover these laws through the study of infrahuman behavior.

This chapter presents a brief summary of the theories, past and current, that have characterized comparative psychology. The presentation will be somewhat more extensive than the usual discussions of theories developed in the study of lower animals. It will include points of view first outlined in respect to human behavior and will show some of their interconnections with interpretations of the infrahuman species. The survey begins with those views that are extremely broad in scope, theories that reflect most directly the philosophical basis on which they were erected, as represented by the work of Plato, Aristotle, and others. We then turn to a review of some of the late nineteenth and early twentieth-century theories. These conceptual formulations by scientists, pioneers in the area, were instrumental in the development of comparative psychology as an independent discipline with its own problems and techniques.

In later sections of this chapter we shall review the main contemporary theoretical contributions in regard to learning. Since the contributions of Hull [17], Tolman [32], Guthrie [15], and Skinner [29] have been presented *in extenso* in other sources, our summary of them will be sharply abbreviated. Our efforts will, instead, be directed toward a relatively more complete survey of possibly less well-known theoretical points of view. These will include (*a*) the influence of statistical theory upon learning and perception; (*b*) the influence of perceptual theory upon comparative psychology, as shown by Razran's [27] theory of conditioning and perception and by the Gibsons' [14] discrimination theory of perceptual learning; (*c*) the neoinstinctual movement as represented by Tinbergen [31] and evaluated by Verplanck [36]; (*d*) the influence of the neurophysiologists upon comparative motivation, with Olds' [23, 24] theory and experimentation representative of this trend; and (*e*) a summary of some influences of field theory (or more molar psychology) in respect to animal behavior.

HISTORICAL INTRODUCTION

Our first task will be to sample the broader philosophical points of view and thus lay the foundation for the more specific theoretical developments. This will necessitate an examination of some of the early Greek philosopher-scientists who were concerned with the nature of the mental and behavioral processes in animals, even though they had not developed the experimental method to study them.

The Greek Philosopher-Scientists

Plato and Aristotle. The general problem of comparing man with infrahumans was dealt with by early philosophers. Plato [26] later advocated a dualistic position in which he maintained that the concept of the soul could be used to distinguish between infrahumans and man. He divided the soul into rational and irrational parts with implications that the latter was further subdivided into nutritive and passionate souls. The nutritive soul was assigned to plants; the nutritive and passionate both were assigned to animals. Man, however, possessed all these different souls located in different parts of the body. For example, the passionate soul was located in the heart. The differences between man and the lower animals were thus explained in terms of these various souls.

The beginnings of the theory of evolution appeared in the writings of Aristotle [1, 2, 3]. He suggested that animals could be viewed as forming a series ranging from the lowest to the highest species. The highest species, however, did not evolve from the lower, but all animals were governed by a perfecting principle, constantly striving to reach a perfect type. He also distinguished among these three souls: the nutritive soul, which governed nutrition and reproduction in all animals and plants; the sensitive soul, which was not found in plants and was connected with sensations in the higher animals; and the rational soul, peculiar to man. Aristotle believed that man's memory was different from the infrahuman's, since man could voluntarily recall the past.

Many of the concepts that are important in contemporary comparative psychology had their origin in the writings of Aristotle. Modern learning theory had its genesis in his works, since he taught that animals have memory and could profit from training. The beginnings of the law of effect were found in the notion that all animals seek pleasure with things that nature holds appropriate. We shall see later in this chapter that the law of effect (with variations) is one of the most important concepts in comparative psychology. The variations of this concept are one of the clues to understanding the differences among the variety of learning and perception theories.

Early Renaissance

The early Renaissance brought forth a systematic comparative model of man in the writings of Descartes [13], to whom may be attributed the beginning of behaviorism. He assumed a dichotomy between mind and body. The soul (mind) was distinct from the body, though it was assumed that mind could control the body through the pineal gland of the brain and direct the flow of animal spirits into various channels. Men had souls but animals did not. The further behavioristic implications in Descartes's writings were in the notion that animals were automata and perhaps even man was not as wholly rational as most people thought.

The Modern Period

Because Darwin [12] viewed mental development from an evolutionary point of view, he was largely responsible for the science of animal behavior. For Darwin, the difference between man and the lower animals was quantitative (considered as a series of very fine gradations). To support this position, he maintained that man and the lower animals have similar sense organs, instinctive responses, emotions, memory, etc. In his day this was a revolutionary idea.

Various individuals attempted to validate this theory of mental continuity between man and animals by means of the anecdotal method (using "stories" collected about the clever behavior of animals). The anecdotal method was a challenge to psychologists and biologists and sent them to the laboratory to study systematically the behavior of animals. The anecdotalists had collected a large amount of information and had made rather broad claims, e.g., that animals used language and had a sense of beauty. Some unsubstantiated assumptions pertaining to animal intelligence were also formulated. An important point to remember is that the experimental method (and the science of comparative psychology) arose largely as an attack upon the bizarre implications arising from the anecdotal movement.

Following the theory of evolution and the experimental attack upon the anecdotal method of establishing psychological assumptions, a host of pioneers emerged who established comparative psychology as an independent science. We shall examine the contributions of a few of these individuals: Morgan's interpretation of the law of parsimony [22], the biological approach of Loeb [20] and Jennings [18], and the theoretical and experimental work of Thorndike [30].

Morgan's Canon. As implied above, the anecdotal method produced a tendency for investigators to anthropomorphize; this resulted when they tried to draw analogies between the human mind and the animal mind. Anthropomorphism is a tendency of man to project his own inner experiences into infrahumans; since he can report for himself feelings and sensations, images and ideas, he assumes that his dog and his cat can feel, imagine, and think.

In order to curb this anthropomorphic tendency among investigators, Morgan [22] proposed his now famous canon. This canon states: "In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale" [22, p. 53]. This principle exerted, and still exerts, a tremendous influence upon comparative psychology. Sometimes this influence has tended to hold back the investigation of the more complicated aspects of animal behavior. It also may have artificially led many times to the reduction of complicated processes to very simple ones. Nevertheless, it made the comparative psychologist very conscious of operationally defining his concepts. In "their simplest and basic form operational definitions specify the measuring operations used to identify phenomena" [35, p. 52]. Both the canon and operational definitions force the comparative psychologist to "take the fuzz" from his constructs.

The Biologist's Approach. The tropistic theory of Loeb [20] was a further demonstration of a revolt against anthropomorphism and an emphasis on objectivity. Tropism was defined as an unlearned orienting response of the organism, resulting in its moving from or toward a stimulus. Heliotropism, the bending of plants toward the source of illumination, and geotropism, a response to gravity, are examples of tropisms. Tropisms were classified as positive or negative in accordance with the response toward or away from the source of stimulation. Loeb attempted to explain animal behavior by physicochemical principles. He even went so far as to exclude such concepts as trial-and-error learning, in fact any description that might imply mental processes in animals. He felt that any other approach to organismic behavior would not lend itself to quantification. Although a great deal of his research was carried out on the invertebrates and plants, applicability to the higher animals, including man, was implied.

The opposition to Loeb's tropistic position was led by Jennings [18], who advocated the theory of trial-and-error behavior. Through experimentation with protozoan forms he was able to demonstrate that their behavior did not always fit Loeb's theory of highly mechanical and rigidly determined organisms. Primitive trial-and-error behavior appeared in organisms when they were presented with various stimuli. Jennings did not accept the assumption that even these simple organisms were automata. Jennings's concept of trial-and-error learning paved the way for the theories of Thorndike, and many of the more contemporary learning theories which will be discussed below.

This conflict between Loeb and Jennings also represents one of the basic conflicts that continues in comparative psychology. For instance, it appears to some degree in the conflict between two current learning theorists, i.e., Hull [17] and Tolman [32]. Hull was avowedly mechanistic, while Tolman describes his system as a purposive behaviorism (see below).

Connectionism. Comparative psychology would be incomplete without Thorndike's [30] connectionistic theory of learning and the experiments he devised to support it. One of his often-cited experiments was quite simple in design. A cat was deprived of food and then placed in a puzzle box, so constructed that the cat could open the door and receive food if it pulled a latch. The cat exhibited trial-and-error behavior, i.e., a variety of movements and responses before it hit upon the correct response (pulling the latch and going to the food and eating it). Thorndike observed that after several repetitions of this performance the cat would exhibit less trial-and-error behavior before it found the latch. He also noted that there was a decrease in the length of time that it took the cat to get to the food.

As a result of the above type of observations, Thorndike formulated his now famous law of effect: If a modifiable connection is made and is followed by a satisfying state of affairs, this connection will become stronger. If, on the other hand, this connection is followed by an annoying state of affairs, then the strength of the connection will become weakened. By a satisfying state of affairs, Thorndike meant those states which the animal would not try to avoid, and by an annoying state of affairs those states which the animal would try to terminate.

Thorndike's theory was significant because it grew from experimentation and was subject to laboratory verification. His most frequently cited contribution to learning theory was his law of effect. It aroused interest in the role of reward (reinforcement), still a controversial topic in contemporary American learning theories.

A SURVEY OF CONTEMPORARY LEARNING THEORIES

Comparative psychology gradually began to lift itself out of a philosophical, anecdotal context. Having grown with such individuals as Thorndike, who contributed techniques of observation as well as laws concerning learning, it departed, unfortunately perhaps, from the comparative approach and settled upon one major problem, i.e., the nature of animal learning. The albino rat became the main "guinea pig" in the somewhat narrow-in-scope experimentation of the American learning theorists. As is considered later, however, an antidote appeared in the work of the European ethologists.

Owing to the limitations of space, we shall cover only four of these current learning theories, presenting briefly some of their basic assumptions. These theories are systematic behaviorism, sign-gestalt, contiguous conditioning, and descriptive behaviorism.

Systematic Behaviorism

Comparative theory emerged from its adolescence in the systematic and highly structured behaviorism of Hull [17]. Similar to Thorndike before him and to the other contemporary learning theorists discussed in this section, Hull was an associationist. His major postulate was that a stimulus and response were associated *if* followed by reinforcement. And a further significant point in regard to Hull's theory was his conception of what was essential for strengthening the associations. Primary-need reduction was the necessary reinforcing condition for learning. In other words, various stimuli in the learning situation were connected to responses *if* they were followed by the reduction of drive stimuli from some primary need (as hunger, thirst, etc.). However, secondary reinforcement could be a substitute for primary reinforcement; Hull assumed that neutral stimuli could acquire such secondary reinforcing properties. As is indicated in Chapter 6, in a typical maze experiment involving a hungry rat and food at the goal, the sight of the goal box (stimuli therefrom) could and often did acquire secondary-reward property.

Not all of Hull's postulates were crucial to his theory. One, as stated above, was the heart of his system: the necessity of primary or secondary reinforcement for learning to occur. Such reinforcement added an increment to habit strength. Another postulate laid the groundwork for his biological theory of trial-and-error behavior and the survival value, in the evolutionary process, of this type of behavior. Another restated one of the fundamental conditions in associative learning, namely, the contiguity between stimulus and response.

Hull, more than other theorists, formally stated his assumptions, applied symbolic logic to them, and presented them in such a manner that they became a model for others. In any formulation of theory today it is expected that the assumptions will be spelled out in detail so that little is left to interpretation, and the assumptions should be testable in the laboratory. In addition to setting a standard for theory construction, he was responsible, directly or indirectly, for many investigations, thus adding much information about animal behavior. His influence will long be remembered.

Sign-gestalt Theory

Sign-gestalt theory, as Tolman [32] outlined it, was the principal opposition to the systematic behavior theory of Hull. This opposition can perhaps be understood by examining the latent-learning experiments which Tolman and his associates attempted to use in supporting their position.

Latent learning is that acquisition which is not evident to the observer while the learning is actually occurring. The psychologists infer it from later performances when the learning curve changes rapidly, owing presumably to the earlier acquisition. In Blodgett's [5] experiment, a group of rats ran a maze and received the reward of food in the goal box. A second group was allowed to run the maze without receiving food in the goal box; then food was introduced after a certain number of trials. The striking result of this experiment was that *when* the initially nonrewarded group received food, its performance almost immediately equalled that of the first which received food all along. Apparently the second group had learned during the nonrewarded trials and later used this learning.

Without all the details of latent learning, as a topic of interest to comparative psychology, it can be pointed out that Blodgett's experiment posed two questions: (*a*) Can learning be latent and later be revealed in performances? (*b*) Can learning occur without a reduction in either primary or secondary motivation?

There was no real controversy between Hull and Tolman in respect to the first question. Both theories permitted a positive answer in regard to the possibility of learning being latent. However, they differed in their predictions in regard to the second question. Hull insisted that no learning could occur without his kind of reinforcement. Tolman replied that this was not essential but possibly useful.

The latent learning controversy stimulated a considerable amount of research. Several variations of the latent-learning design were used. MacCorquodale and Meehl [21] proposed a classification of the different latent-learning experiments.

In the first class, the animals ran a series of *unrewarded trials with later introduction of the relevant reward.* Blodgett's experiment, previously discussed, is an example of this type of experiment.

Another type was classified as *location of incentives learned under satiation and tested under relevant drive.* Animals satiated with food and water were allowed to run a T maze which contained food in one arm and water in the other, but no primary-need reduction occurred. Latent learning was demonstrated on later test runs *if* the "hungry" or "thirsty" animal chose the appropriate turn to reach the relevant goal.

The *learning of incentives under strong irrelevant (competing) drives* was another classification of the latent-learning design. Food was placed in one arm of a T maze and water in the other arm. By a forced-run procedure animals were given equal practice on both sides of the T maze. Let us say the animals were hungry but not thirsty. The problem was whether such animals would later enter the proper arm *when they were thirsty.* Would they perceive where water could be found during the trials when they had no need for it? The results were controversial, but some support was given to Tolman's assumption that learning could occur without drive reduction.

Tolman, more than any other contemporary theorist, held that animals *perceived* far more than was apparent to the investigators. He assumed that latent learning could be the acquisition of perceptual lore and used later. In many respects the latent-learning problem was the catalyst for an emphasis that continues in comparative psychology, namely, an emphasis on perceptual-type theories rather than on stimulus-response theories of learning. Later in this chapter we shall examine some of the perceptual theories including one formulated from observations of man. The relationships among human perception, animal perception, and learning theories are important, in that they contribute toward an answer to the fundamental problem of comparative psychology, i.e., an understanding of the differences and similarities between man and infrahumans. This point will be reexamined later.

The comparison between Hull and Tolman should include one final point. Hull assumed that associations were formed between stimulus and response. Tolman did not ignore the response, but learning for him was the association of one stimulus (S_1) with another (S_2). In other words, the learner acquired an expectancy that if he responded in a certain manner to S_1, then S_2 would follow. What was learned was a sign-significate relationship (a sign gestalt). Tolman's view of learning led him to assume, as an intervening event, the acquisition of a cognitive map (a temporal-spatial "picture") by a rat traversing the paths of a maze.

A Theory of Contiguous Conditioning

The theory of contiguous conditioning proposed by Guthrie [15] depends upon association of stimuli and responses. The essential condition necessary for the association of stimuli with responses was simultaneity, i.e., if a stimulus and the response were presented together, they became associated.

In order to explain "non-simultaneous conditioning," such as trace conditioning, Guthrie proposed that the stimulus set off a chain of movements, occurring in the time interval between the onset of the conditioned stimulus and the response to be conditioned. Acting as cues, these movements could be head responses, orientation toward the food, etc. In other words, the animal would make certain responses which served as stimuli for further responses, and *the last of these movement-produced cues were thus associated with the final conditioned response.* These intervening movements filled in the time gap between the stimulus and response to be associated.

Reward was treated as a secondary principle in Guthrie's system, rather than a basic principle, as formulated by Thorndike and Hull. According to Guthrie, the reward only served to direct the animal in such a fashion that the appropriate stimuli would become associated and remain so associated with the proper responses. For example, in Thorndike's study, reported above, of the cat learning to pull the latch to get out of a problem box, Guthrie would *not* assume that the obtaining of the food reward reinforced its associations. Rather, the food reward was effective because it took the animal away from the prefood situation, thus shielding the stimuli in that situation from associations with new responses. The stimuli from the latch string would be the last to be associated with the responses of leaving the puzzle box. The necessary learning condition would be thus met, i.e., the condition of the simultaneous association of the correct stimuli with the correct responses. The food reward was considered useful but not essential to this association. Reward did not directly strengthen the associations of stimulus and correct response, but it prevented them from being unlearned. As can be inferred from the above, Guthrie postulated one-trial learning between stimulus and response. In order to interpret the slowness of complex learning, Guthrie pointed out that not all of the necessary stimulus cues were present in any one trial and thus could not be associated with the proper responses; hence, several trials were often necessary for all essential stimuli to be associated with the correct responses.

Descriptive Behaviorism

Skinner's [29] descriptive behaviorism aided considerably in restoring the balance between theory and the laboratory. In essence he asked the psychologists to drop their pet hypotheses, go into the laboratory, and record behavior. He distinguished between two general classes of behavior: (*a*) the respondent, elicited by experimentally isolated momentary stimuli; and (*b*) the operant, not so elicited but emitted by the organism. In operant conditioning the stimuli which produce the behavior are not isolated by the experimental observer. A great deal of behavior on the human level may be classified as operant, such as driving automobiles. A typical example of a respondent is the elicitation of a flow of saliva by food placed in the mouth, as in Pavlov's conditioning studies.

Skinner, most interested in operant behavior, devised a method of recording it. This device—the Skinner box—is now a classic in psychological methodology and is used in a great many areas of psychology. The subject is placed in a closed external field, as a box, and allowed to press a pedal or push a lever or similar device; he then receives a reward such as food. The apparatus is so constructed that exact measures can be obtained of the amount of objective reward, the number of pressings (or other operant behavior), as well as the temporal relations between them (the schedules of reinforcement). A reward may follow every operant response, or a pattern of intermittent reinforcement may be used.

The particular schedule of intermittent reinforcement used may be a fixed ratio, a fixed interval, or a variable interval. Fixed ratio refers to reward being given after a certain number of emissions of the operant, e.g., after five or ten pushings of the lever. Fixed interval refers to a schedule of reinforcement arranged on time intervals, such as after each minute or some other time period. With the variable-interval schedule the reinforcer follows a changing time schedule.

Skinner's contribution to comparative psychology is not in theory; his extraordinary results from animal training with pigeons, rats, and monkeys suggests that he has a methodology that "works." His animals have done things which members of their species have never done before. Skinner claims that it is not that their forebears were incapable of such behavior; rather, nature simply never arranges effective sequences of reinforcement schedules for the unusual behavior which Skinner is able to shape in the different species.

It should be noted that Skinner *indirectly* raises an important problem for comparative psychology, a problem previously stated above: the comparison of the various levels of animals in respect to learning, perceiving, conditioning, remembering, etc. Though not himself interested in the central processes which *may* be inferred as occurring in his animal subjects, nevertheless his experimental findings raise certain theoretical questions of interest to comparative psychology. Since the behavior of the variety of animals (including man) subjected to operant conditioning is apparently shaped by the same methods of training, a question arises: Do all animals have the same central processes during their training? If we assume that all organisms are capable of perceiving, at least organisms of the higher level, do they perceive their external fields in the same way? Such questions, however, are not raised by Skinner, and his system does not give any direct answer to them. It is possible that the behavioral records which he and his followers are accumulating may, in time, aid in answering these or similar questions.

Some theories useful in setting up studies of the important central process of perceiving follow in the next sections. The first are statistical theories of learning and perception, applicable to infrahuman and human species. Then follows a point of view on conditioning and perception and finally, a perceptual theory developed from observations of the human species.

SOME THEORIES OF PERCEPTION

A Statistical Theory of Perception

Brunswik [7, 8] was critical of the artificial environment of the laboratory studies of perception. He pointed out that in the experiments on discrimination, with such an animal as the rat, controls were usually attempted so that reward was associated with only one cue and not with others. In a simple black-white discrimination, for example, only the response to the white card might be rewarded. Such a simplification of the perceptual situation, he stated, was not encountered in life situations. Similarly, the experiments with human subjects were greatly oversimplified as contrasted to daily-life perceiving. For example, in size perception the higher organism when perceiving in the usual life situations makes use of many different cues—convergence, accommodation, brightness, etc.—combined in different ways. The final perceived size of an object may depend upon a small retinal image combined with a cue for distance or upon a large retinal image for a short distance. Brunswik pointed out that the laboratory experiments tended to ignore the complexity of simultaneously present cues upon which perception normally depends.

Brunswik was interested in determining how the organism could perceive and attain objects in its usual external field in spite of the great variety of constantly changing stimulus conditions. He assumed that the perceiver had to use all the data available to it, in conformity with what were described as the laws and demands of biological adaptation. Because of the complexity of the external field, accurate perception was always a probable achievement. Brunswik implied that the subject might be thought of as a statistical machine testing certain hypotheses which differed in the probability of their confirmation if acted upon. In a simple black-white discrimination problem, assume that the rat behaved as if the white card were the one to respond to. How was the rat perceiving the white card? According to Brunswik, the white card had acquired (for the rat) a higher probability value of leading to the food than the black card. Likewise, in size perception it was assumed that the individual organism weighed the probabilities of all the various cues, and the final combination of them was the perception of the dimensional magnitude of the object in question. Thus the maintenance of veridical (true)-distal (distance) relationships with objects in the external environment depended upon the statistical validity of cue-to-object relationships, and the validity of these cues was determined, but limited, by a very changeable external environment. The accuracy of the perception was therefore a probable achievement.

In summary, Brunswik advocated that the investigators of perception obtain statistical samples of the various cues in the usual life conditions of organisms. He suggested viewing any organism as a whole and determining what objects it attained by perception and action. He was not very much concerned with how this took place.

In our present review of theories it is not necessary to consider the pros and cons of Brunswik's position. Its importance lies in the fact that it furnishes comparative psychology with a possible model for interpreting perceptual learning both of humans and infrahuman subjects. Perhaps Brunswik's theoretical position will be clearer if we now examine a related statistical theory of discrimination learning, designed particularly to interpret the behavior of infrahumans.

A Statistical Theory of Discrimination Learning

The simple discrimination problem was also utilized by Restle [28] in illustrating his theory of discrimination learning. As indicated above, in this type of experiment the animal is trained to discriminate between a black and a white card. Assume that the food is always behind the white card but this card is moved in position, sometimes to the right, other times to the left. Thus, the animal may respond to at least three possible cues: the whiteness, the blackness, and the position of the cards (right or left).

In the learning to solve such a discrimination problem, it was assumed by Restle that two processes occurred. (*a*) The subject learned to make the appropriate responses to the white card, consistently reinforced and hence a *relevant* or valid cue; the process which permitted this learning was called *conditioning.* (*b*) The animal's responses also became independent of the other cues, such as position or blackness. These were *irrelevant* or invalid cues, since they were not consistently reinforced. Suppressing the invalid cues was the second process and was called *adaptation.*

Restle described the total situation that the animal faced in such a discrimination problem as a "set of cues." The animal had to learn to make differential responses to them. Relevant cues were used by the animal to predict where or how the reward was to be obtained. (Remember that an irrelevant cue was one which might, at times, be associated with reward but not systematically.) The various cues acquired degrees of probability of being correct (rewarded), but the white card, the valid cue, acquired a higher probability value of being rewarded.

In summary, the animal, according to Restle's theory, had to learn to differentiate cues, and this differentiation took place according to the two processes described above (conditioning and adaptation). Finally, the valid cue acquired a higher probability value of being correct.

An important point of comparative psychology is that the theories of both Brunswik and of Restle permit an examination of infrahuman and human subjects from a common frame of reference.

A Theory of Conditioning and Perception

Razran [27], in considering the problem of the relation of conditioning and perception, proposed four types of conditioning.

The first type was called *conditioning without perception.* Subliminal conditioning was an example of this type. The conditioned stimulus and the unconditioned stimulus were below the threshold of consciousness for the individual, and yet conditioning took place. Other illustrations in this category were spinal conditioning, subcortical conditioning, or any conditioning occurring very low on the phylogenetic scale. Note that it was not assumed that either the unconditioned reaction or the to-be-conditioned reaction involved perceiving. In other words, Razran suggested that in both animals and man learning existed that was nonperceptual; this learning was thought of as cellular rather than central and protoplasmic rather than perceptual.

The *conditioning of perception* was a second classification. This was illustrated by a salivary conditioning experiment. The subjects, while eating and hence salivating, were presented with the sound of a metronome. They were not told, however, that they were being conditioned or that there was any relation to be formed between eating and the metronome sound.

The third type was *conditioning through perception.* When this occurred, as it might in a salivary experiment, the subject was aware of both the conditioned metronome and the salivary response and was also aware of the relations between the two, i.e., of the conditioning possibilities between them. Razran described this third type as perceptual or relational learning, because the subject was said to be aware that a connection was being formed.

The fourth type was *perception through conditioning.* The following experiment illustrated this kind of conditioning. A subject's primary drive, such as hunger, was rewarded with food while he was engaged in some activity involving perception, e.g., listening to music or looking at paintings. The subjects were asked to write down their reactions to the music and the pictures before, and then after, the food was received. The subjects changed their reports after the eating was associated with the music and art forms. They responded in a manner more similar to experts. Their reactions were less stereotyped. The changes that were noted in their perceptions, according to Razran, resulted from the interaction of the affectivity aroused by the food with the affectivity resulting from the music and the paintings. He suggested that these changes (learning) reflected a higher perceptual integration than was present in other perceptual changes.

Razran's contribution is that he suggested some differences between humans and infrahumans in respect to psychological processes. His first type of conditioning could apply to the lowest organism on up to man. Note, however, that the fourth type is more applicable to man. An amoeba, while eating, cannot listen to Bach's music and thus have a "higher perceptual integration." Whether Razran's conclusions are correct or not, the suggestions he made are of some significance in phylogenetic comparisons.

A Discrimination Theory of Perception

It is important to examine theories of perception as developed from the observations of man in order to determine their adaptability to infrahuman problems. The Gibsons' discrimination theory has been selected as one with possible implications for comparative psychology.

The following experiment reported by Gibson and Gibson [14] illustrates many features of their theory. Subjects were presented with a series of nonsense scribbles, line drawings with no or little form. In other words, the subjects were presented with a series of unstructured figures, most of which, at first glance, looked alike. One was designated as the standard, and four copies of this were shuffled into a pack of cards marked by similar drawings. The subjects first examined the standard drawing. Then they were presented with the total pack of cards. The instructions were to identify the standard cards. Since most of the drawings looked alike, the subjects, children and adults, had to learn to differentiate between the standard and the other figures. This experiment illustrated that a stimulus item (the standard drawing) might at first be indistinguishable from a whole class of items in some stimulus universe tested, but with completed perception the item is differentiated from all other items.

How does this differentiation occur? According to the Gibsons' theory, percepts change over time by progressive elaboration of features and qualities of the stimulus items. In the above experiment, the subjects learned to point to and label certain features of the individual line drawings. Such features were described as "too thin," "curl," "rounder," "reversed," etc. This was interpreted as follows: Perceptual experience reflects the objective world. In other words, a percept is *not* composed of sensations and images as older theories often implied. As perception develops, more and more properties of the objects become distinctive. If perceptual learning is successful, the phenomenal properties and phenomenal objects correspond to physical properties and physical objects. The experience thus is in greater, not less, correspondence with stimulation. This change is evident in the above experiment when the drawings, at first appearing much alike, are later distinguished from each other. The distinctive features of the different drawings emerge and also the features of the standard drawing. One other point, emphasized by the Gibsons, is that perceptual learning consists of acquisition of responses, i.e., new features of the physical stimulation are responded to. In other words, perception may be thought of as getting in closer touch with the environment.

It is obvious that this discrimination theory has implications for infrahumans, because it deals with responses (not with images) and also deals with physical stimulation in the external environment. The source of this stimulation can be manipulated by an experimenter, and various hypotheses in regard to subhuman perception can be tested. The previously discussed experiment with unstructured drawings could even be adapted for infrahuman subjects. A hungry animal could be placed in a discrimination apparatus with different doors marked by the different drawings. The animal would receive food when he entered the door marked by the standard drawing. The problem, therefore, would be to get the animal to differentiate the standard from the other cards. This problem would probably be too complex for infrahumans if many figures were used. What is important, however, is that the Gibsons described a set of experimental operations which will permit comparisons of perceptual response change as exhibited both by infrahumans and by humans.

The above theory points up certain possible similarities between man and infrahumans in the perceptual process but does not account for an important difference between them. As the Gibsons state, their theory does not deal with subjective phenomena, such as images and hallucinations, which man reports. These subjective phenomena can only be studied by introspective techniques, obviously not applicable to animals below man.

We have been suggesting that learning and perception be viewed as one process, i.e., discrimination. And second, it was suggested that man and infrahumans are probably similar in this process of discrimination. However, they may be different in their capacity for subjective experience. Of course, the variables operating in human discrimination are far more complicated than those in subhumans.

NEOINSTINCTUAL THEORY

The European Ethologists

The European ethologists or naturalists, such as Tinbergen [31], have challenged the emphasis placed on learning by the American theorists. One of their many interesting observations is in the report of the hunting reaction of the water beetle, a reaction dependent upon what is called an inherent sign or cue stimulus. The beetle was presented with a tadpole enclosed in a glass tube, but the hunting reaction was not released since the beetle could not smell or touch the tadpole. When, however, a watery meat extract was released *directly into the water*, the beetle started to attack almost every solid object with which it came in contact. A significant point was that the essential chemical sign, the stimulating agent, had to be present to elicit the instinctive hunting response. A similar observation was made of the sign necessary to elicit the aggressive reactions of the male stickleback fish. In the spring the male stickleback fish has a very red throat and belly, and during this season the male fish will attack one another. In attempting to isolate the necessary sign that aroused this aggressive reaction, Tinbergen used models of fish. The first models looked like fish in form, but the color was removed. Second, the form was drastically changed, ranging from oval to thin, elongated shapes, with some models having the red color on their chins and bellies. The stickleback tended to respond much more vigorously to the models with the red on them regardless of shape, thus demonstrating that it was primarily the color that released this instinctive aggressive reaction (see pp. 56–60).

One of Tinbergen's contributions to theory lies in his principle of *selectivity*. In the observation of the water beetle, note the selection of chemical stimulation out of other potential sensory inputs. Also, the stickleback fish selectively responded to color rather than to form. In the conventional investigations of sensory capacity of animals, the observer can deduce what cannot be sensed by the animals but often cannot be absolutely certain as to what releases reactions. Tinbergen's studies, however, demonstrate clearly that animals do not react to *all* of the environmental field.

Tinbergen reported that in general the animals respond blindly to only a fraction of the total environmental situation, neglecting the other aspects. This happens in spite of the fact that the animal's sense organs may be perfectly able to receive the neglected stimuli. Excitatory components of the external field may often seem significant to the experimenter but are not necessarily the ones that an animal actually reacts to. Mistakes are easy to make in interpreting the "signs" in the external world necessary to elicit a particular behavior from a subhuman subject or, for that matter, from human subjects.

Tinbergen also suggests that animal behavior is partly due to *nonselectivity*. Organisms may exhibit a *lack of discrimination* for a wide range of stimuli, i.e., the water beetle, when the hunting reaction was released, attacked almost every solid object that it contacted. Such errors, according to Tinbergen, are an important feature of instinctive behavior.

Tinbergen does not neglect the internal factors and conditions that are involved in selective release of instinctive organizations. Within certain limits there is a positive correlation between the magnitude of the liminal stimulus and the amount of time that passes after the last feeding or the last coition. The "internal" factors may be so strong that the motor responses break through when there is an absence of a releasing stimulus. The influence of the internal factors may also be inhibitory of the effects of certain types of stimuli, such as is observed in the inhibition of reproductive activity in birds when the temperature is lowered.

The European ethologists revived an old problem: the instinctual interpretation of animal behavior. This problem periodically manifests itself upon the psychological scene. Broadly stated, the theory holds that certain behavioral patterns are genetically laid down in the nervous system. In the instinctive view of behavior, learning is often quite incidental; it is assumed that the behavioral patterns tend to unfold in a fairly orderly sequence because the organism is so organized by gene influences.

The work of the European ethologists has not gone unchallenged by American psychologists. Our next step will be to examine a criticism of the ethological approach.

An Analysis of the Ethological Approach. For Verplanck [36], the distinction between learned and innate behavior is an absurd distinction, such as would be made if physicists distinguished between light that is made up of corpuscles and light which is made up of transverse vibrations. He first questioned the usual characteristics defining innate behavior, i.e., stereotypy, universality of appearance, orderliness, adaptivity, and resistance to modification. He suggested that all criteria of innateness failed except one, the first opportunity that the behavior had to occur without any previous learning. He concluded, however, that no meaningful distinction could be drawn between learned and innate behavior (see Chap. 3).

For Verplanck, the same experimental variables should be operating in both learned and unlearned behavior. Both learned and unlearned behavior should fit the same theoretical structure. Also, the behavioral phenomena observed by the ethologists in the field should be observable in the apparatus employed by the comparative psychologist. And finally, behavior that is studied in the laboratory by the psychologist should be capable of being observed in the field, i.e., under more natural conditions. Verplanck maintained that the ethologists have not adequately isolated their "innateness" from other variables such as species differences, etc.

In spite of his criticisms of the ethologists, Verplanck conceded that they have made important contributions to comparative psychology. From their work has come an increased interest in the behavior of a variety of species, an emphasis on new drives, and new organizations of behavior. The ethologists have emphasized the value of permitting the animal subjects to manipulate their natural environment rather than to force them through mazes or bind them on conditioning apparatus. More freedom for animal subjects would allow behavior to occur that has not been previously recorded, thus broadening the inductive basis, the experimental underpinnings of all theories. In summary, Verplanck recommended that animal psychologists proceed in their experimentation in a manner similar to the ethologists, limiting hypotheses, but making broader observations, trying to record everything that the animal does.

A NEUROPHYSIOLOGICAL THEORY OF MOTIVATION

The role of the nervous system has been largely omitted in the previous discussion though the neurophysiologists have made considerable strides, as in mapping out some of the motivational and reinforcing properties of the brain. The following, therefore, includes a few of the findings and theoretical implications of this approach to animal behavior.

Olds' Theory of Brain Stimulation

Olds [23, 24] and others have performed some interesting experiments in which the animals were motivated by electrical stimulation applied to certain subcortical regions of the brain. The animals (rats), with electrodes implanted in certain parts of the limbic system of the brain, were placed individually in a Skinner box (see Fig. 13-1). When the animal pressed a lever, it would receive electrical stimulation in a neural area. Such experimenting led to the following findings: (*a*) There were various places in the lower centers of the brain where electrical stimulation served as a reward, in the sense that the animal stimulated itself over and over again in these areas. (*b*) There were also areas in the lower brain centers where an avoidance reaction was elicited; if the animal stimulated itself in these areas, it discontinued the pressing of the lever, apparently in order to avoid the stimulation. (*c*) The septal area was one of the first of the isolated neural regions having positive reinforcement when stimulated. (*d*) After stimulation of what were called neutral sites, the animal did very little to avoid or obtain further stimulation (see Chap. 12).

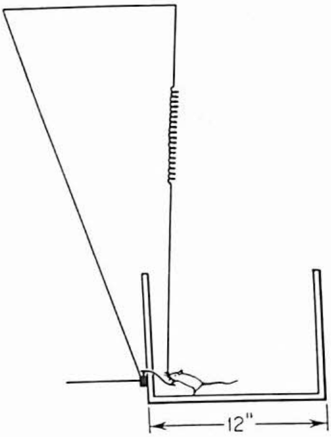

FIG. 13-1. A diagram showing the rat pressing a lever, as in a Skinner box, and receiving electrical stimulation to the brain instead of receiving food. [*From James Olds, Physiological mechanisms of reward. In Marshall R. Jones (ed.), Nebraska symposium on motivation. Lincoln, Nebr.: Univer. of Nebraska Press,* 1955.]

Olds, in attempting to interpret these findings, postulated a reward-punishment dimension with the middle of the dimension being neutrality. If the animal's tendency to stimulate itself were zero, the stimulus would be located on the extreme end of the punishment scale. If the tendency were low, in that the subject neither approached nor avoided the lever, the stimulus was said to be neutral. Reward was defined by the tendency to press the pedal and receive stimulation. Note that the particular stimulated locations in neutral areas were determining reward, neutral, and punishment effects, as defined by performance.

Olds [24] initially suggested that his studies refuted the drive-reductionist's position on learning (see Hull's position on p. 383). The drive-reduction theory of reinforcement considers reward as the reduction of some form of drive stimulation acting upon the organism. Olds stated that his findings demonstrated that it was possible to reward an animal without removing some physiological need. The animals would not perish without electrical input to the septal area of the brain. They certainly had no need for the stimulation. He also suggested that it was unlikely that electrical excitation of the septal area produced the opposite of excitation, i.e., produced drive reduction. Thus he believed that he had demonstrated that reinforcement could be obtained by means of the *addition* of a strong stimulus and that this finding refuted the drive-reduction theory.

The experimental work of Brady and Nauta [6] and others suggested a different interpretation of Olds' findings. When they removed the septal area from a group of rats, the animals became more active, thus indicating that the function of the septal area was possibly to *quiet* the animal. At least it seemed reasonable to assume that the tension in the organism might actually be reduced when the septal area was stimulated. (In another report, Olds [23] accepted this and other possible interpretations.)

Summarizing *all the previous discussion*, we note that the historical background showed how the comparative psychologists finally settled upon the study of behavior in the highly structured laboratory setting. Moreover, to a large extent, laboratory observations were confined to noncentral aspects of the organism, inevitably ignoring the nonobjective processes as perceiving. This resulting rigid behavioristic curtain was, however, broken through by such men as Tolman. A second breakthrough came with the study of the nervous system in relation to motivation and reinforcement. The final section, "Field Theories," could be called a climax to the development of comparative psychology.

FIELD THEORIES

In this section a brief discussion of Tolman's concept of *behavior-space* is used to illustrate field theories. A special topic also developed below is relative reinforcement. In the older view of reward (or reinforcement), it was considered as an isolated phenomenon. This older view is contrasted to the view of reward as relative to the context in which the organism is functioning.

A Theory of Behavior-space

As already noted, investigators often study only one part of the organismic process; e.g., in observing the lever pressing of the rat in the Skinner box, only the relationship between food and bar pressing may be studied. Tolman [33], however, asks us to look for all forces operating in the total situation. For Tolman, the act of pressing the lever is the final result of many forces (called field forces), each of which must be experimentally isolated.

Tolman was influenced by Lewin [19], an important member of the gestalt school, who was responsible for the development of field theory in psychology. Lewin, opposed to the stimulus-response psychology, postulated that the behavior of the organism at any one moment was a function of forces both attracting and repelling. These forces were part of the organism's psychological environment, or psychological field. In order to describe such assumed forces, he set up a language of field theory. "Valence" was one of the many terms utilized. If an object in the environment had positive valence, the individual was attracted toward it. If the object had negative valence, he was repelled by it. Lewin, in using such a term as "valence," considered it a psychological but not a physical force. Life space was defined as the individual's interpretation of the objective environment. Since the concept of life space was not suitable for infrahumans, Tolman utilized a related concept, behavior-space, employing diagrams similar to Lewin's to illustrate it. Figure 13-2 is merely a pictorial description of the assumed forces determining the behavior of an organism, in this case of a rat in the Skinner box. The animal, represented by "Actor," is said to discriminate itself in the presence of the discriminated lever (Lr). The immediate presence of the lever is represented by the pair of dotted lines which connects the actor to Lr.

The concept of expectancy is central in Tolman's description of the rat's behavior; in this illustration, the expectancy may be considered as an acquired set of the animal that he will receive food when he presses the lever. The strength of this set is in part a function of how frequently

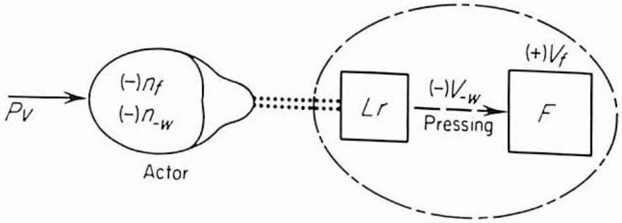

FIG. 13-2. One of Tolman's behavior-space diagrams. It is assumed that the rat presses the lever for food in the Skinner box. The expectancy of food, after lever pressing, is 90 per cent certainty. [*From Edward C. Tolman, Principles of performance. Psychol. Rev.*, 1955, **62,** 315–326.]

the animal has received the food. The lever (Lr), by learning, becomes a sign in the activated expectancy; in other words, the lever becomes a cue that pressing it will bring food. The contents of the dash-dot ellipse represent the whole expectancy. The assumption is made that the animal has acquired an expectancy, or certainty, of about 90 per cent; this means that, if the actor (rat) responds by pressing the lever, he expects to attain the food (*F*).

One of the other forces assumed in operation in behavior-space includes the activated drive (need push) for food which the actor possesses, represented by (−) N_f. The degree of work or effort which, according to the learned expectancy, will be necessary to press the lever is represented by the length of the arrow labeled "pressing." The rat also has a need to push against work represented by (−)N_{-w}. The magnitude and direction of the to-be-predicted performance of pressing is represented by the vector (*Pv*). The performance vector results from all of the following: the need push for food, the positive valence of the expected food, the need push against work, and the negative valence of the expected work. As stated, the performance vector designates the magnitude and the direction of the to-be-predicted performance. If the valence of the expected food is great and also if the expectancy that food would result from pressing is strong, then the greater is the magnitude of performance vector toward actually pressing the lever. On the other hand, the greater the negative valence of the expected work, the greater the need push against work, and the stronger the expectation of work, the less is the performance vector toward pressing.

Tolman maintains that behavior-space is a method of representing relationships such as discussed above; he makes no claim, however, that it is a mathematical system. He also states that it is not so much an attempt to explain concrete responses as it is an illustration of generalized performance. Behavior-space diagrams are neither a picture of the actual geographic environment nor a picture of the phenomenological experience of the organism. They are a pictorial way of representing the interactions between inferred activated central dispositions and their influence on the to-be-predicted performance. They are useful for a holistic description of infrahuman behavior. Certainly a marked contribution of field theory, as exemplified by Lewin and Tolman, is a broader interpretation of performance than is given in the stimulus-response descriptions. Field theory thus is probably a more adequate interpretation of the total organismic process.

Relative Reinforcement

In the previous examination of contemporary learning theories, reward was considered as if it were an isolated phenomenon. In this section we shall examine reward relative to the context in which it arises. This context may include both the condition of the animal and the stimuli surrounding the specific external stimulus object or place which becomes a reward. Previous rewards may also affect the "value" of some immediate reward (see Chap. 5, p. 114). What will be rewarding today is relative to what was previously received.

Perkins [25] outlines some of the more obvious aspects of relative reinforcement. He discusses the condition of the organism as a determinant of what shall be rewarding, e.g., water becomes a reward when the organism is in a condition of thirst. Food is more of a reward in the context of hunger than of thirst. In other words, there is abundant evidence to indicate that what is rewarding and what its influence on learning is depend upon the condition or state of the organism.

Since reinforcement may be viewed as relative to the field, an important problem arises, namely, the measurement of reinforcement. A tentative answer may be obtained by means of the psychophysical methods.

(*a*) How much does the reward have to be increased before there is a significant change in performance? (*b*) Is not the critical (significant) increase relative to the state of the organism? These are some of the questions involved in the measurement of relative reinforcement.

Campbell [11] employed psychophysical methods in his demonstration of relative reinforcement. He subjected different groups of rats to a discrimination problem. The animals learned a preference for the side of a tilting cage where they received a reward, i.e., a smaller amount of a noxious noise. Campbell first determined the amount of reduction of the noise level that would be followed by a 75 per cent preference for the side of the cage with the less noxious auditory stimulation. He called this 75 per cent preference a just-noticeable difference in performance. By studying different groups of animals (each under a different noise level), he found that the amount of reduction of the level necessary to obtain a just-noticeable difference was proportional to the noise level just preceding the reduction. These proportions were not very different from group to group. The small differences in the sizes of the proportions indicated that the reinforcement fraction was similar in constancy to the Weber fractions obtained in judgments of lifted weights or of brightness with human subjects. As in other psychophysical studies obtaining discriminal thresholds, he found that the greater the level of noise to begin with, the greater the absolute change had to be in order to get nonchance change in performance. Guttman [16] approached this same problem of reinforcement threshold by utilizing a different reward and apparatus than Campbell. Using the Skinner box, he gave rats different concentrations of sucrose as reward. He was interested in changes in reward that would bring a just-noticeable difference in bar pressing. He suggested that the psychophysical technique be utilized with other rewarding agents on the assumption that a systematic pattern might emerge among thresholds.

Caldwell [9, 10] also considered within his field theory the hypothesis that reinforcement thresholds follow the Weber-Fechner fraction. He suggested that it be tested on a wide range of stimuli, such as light and temperature, with a variety of different species and recording devices—mazes, activity wheels, Skinner box, discrimination apparatus, etc. The following is an abbreviated form of this hypothesis as applied to a maze-learning experiment when the drive is noxious light and reward is some reduction in light: an increment in the difference between the stimulus strength in the maze and that in the goal box, an increment necessary to produce a significant change in time and errors, is a constant fraction of the previous difference in stimulation between maze and goal. The above might be tested as follows: a certain intensity of light would be present in the maze, then followed with a reduction in the goal box. The problem would be to find the reinforcement thresholds by observing significant changes in behavior following various amounts of absolute reduction. (Different groups of animals would have to be tested.)

The psychophysical treatment of relative reinforcement is not only important in its own right, but it has broader implications for comparative psychology. It provides a quantitative basis for comparing the different organisms. Are reinforcement thresholds the same for man, monkeys, and rats? Such a question, when answered, should lead to new phylogenetic comparisons.

SUMMARY

The early philosophers such as Plato and Aristotle laid the groundwork for later investigations of infrahuman behavior. They raised the problem of comparing man with infrahumans on the basis of souls of differing complexity. Darwin's concept of "mental continuity" from the lower animals to man led to the anecdotal method which in turn provided the stimulation for laboratory investigations of animals. Loeb, Jennings, and Morgan were pioneers in the establishment of comparative psychology as an independent science. The controversy raised by the contrasting views of Loeb and Jennings concerned the mechanistic versus the nonmechanistic interpretation of animal behavior. Morgan gave comparative psychology his interpretation of the law of parsimony, which curbed the tendency of observers of animals to anthropomorphize.

The development of different concepts of reinforcement or reward was one of the dominant themes running throughout the many theories of behavior. Thorndike, with his operational statement of the law of effect, turned the comparative psychologist to laboratory investigations of the problems of reinforcement. The concept of reinforcement, as variously interpreted, permitted comparisons among the theories of Hull, Tolman, Guthrie, and Skinner. For Hull, reinforcement (as drive-stimuli diminution) was essential to the learning process. He maintained that if stimulus and response connections were to take place, they must occur in temporal proximity with reduction of drive stimuli. Tolman maintained that learning was not just the establishment of stimulus and response connections followed by drive reduction; learning was the establishment of associations between stimuli leading to formation of cognitive maps. Reinforcement was not essential for learning but a determiner of performance. Guthrie followed Tolman in his underemphasis on Hullian-type reinforcement, advocating the principle of contiguity of stimuli and responses as the essential condition for learning. Skinner made use of the reinforcement concept in maintaining that the strength of an operant response would be increased if it were followed by a reinforcing stimulus. Olds and others opened the door to the possible neurological correlation of drive-reduction phenomena. They showed that the brain contains what appear to be reward centers. Animals will seek stimulation in these areas as persistently as they will seek food or water.

The European ethologists challenged the American learning theorists, presenting evidence that not all animal behavior was due to learning. Unlearned behavior would appear if the appropriate (sign) stimuli were presented to the animal. Verplanck challenged the ethologists, pointing out that this so-called "instinctive" behavior could be considered as another drive to be studied in the laboratory and that the distinction between learned and unlearned behavior was absurd.

Views of reward changed with the influence of field theories. Earlier, reward was viewed in absolute terms (as quantity of food) rather than as relative to the context or field. Tolman's theory of behavior-space was based on the assumption that forces in the field, including the reward (positive-valenced object) acted as determiners of the final performance of an animal. Campbell and others obtained evidence to show that the amount of reward necessary to produce a just-noticeable difference in behavior tended to be a constant fraction of the drive stimulus. Limited evidence indicated that reinforcement thresholds resembled the Weber-Fechner fraction.

In the contemporary learning theories, with the exception of Tolman's, perceiving was ignored. Though it might, at first glance, appear absurd to attempt phylogenetic comparisons in respect to perception, several theories were presented with suggestions for investigating differences and similarities in this process. Razran, in his four types of conditioning and perception, tried to show where conditioning left off and the unique features of human perception possibly began. Brunswik and Restle, by viewing the organism as a statistical machine, presented a model which was applicable to both man and infrahumans. The perceptual theory of the Gibsons was deliberately chosen as one developed on the observations of human subjects but also applicable to infrahuman subjects. They pointed out that there was one aspect of human perception which their theory did not encompass: the introspective reporting of images and signs of hallucinations in humans. It is possible that these and related phenomena distinguish man from infrahumans, rather than the capacity to make discriminatory responses to external stimulation.

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CHAPTER 14

Research Trends in Comparative Psychology

INTRODUCTION

In this chapter we shall attempt to describe current trends of research in the field of comparative psychology. In doing so, we shall consider not merely the more "pure" form of comparative study but all studies done either by psychologists or biologists that involve animals.

What are research trends? Broadly speaking, they are the main directions taken by researchers in a certain area. In comparative psychology, such directions can be specified not only with respect to kinds of problems being studied but also with respect to countries engaged in animal research and the types of animals used in tackling particular problems. While all these aspects of trends will be touched on in this chapter, the first aspect, that having to do with types of problems, will be developed more fully.

For the most part, our survey will cover studies done within the last ten years, though occasionally we find it necessary to refer to earlier work that is particularly important. Assessing trends is not an easy task. Certainly, one indication of a trend is given by the quantity of work being done on a particular topic. For example, during the 1940s much effort was devoted to the investigation of audiogenic seizures in rats, and accordingly, the work represented a real trend in the literature on animal behavior. Sheer volume is not the only indication, however. Very often studies done in a variety of different areas may share some common point of view or approach that is not obvious from cursory inspection. Such a trend may remain hidden from the researchers themselves for a long time, until it finally emerges and a major break-through is made. Much of the fascination in looking at research trends lies in the hope of uncovering such communalities by the close exploration of apparently different lines of work.

The main bulk of the research with which we shall deal comes from

America and Europe. This will not give as one-sided a picture as one might think, since the largest proportion of all animal-behavior studies done in the last decade comes from these countries. We shall still refer to work from other places when necessary, however.

Before discussing specific problem areas, let us first look at the general state of the whole field of animal behavior. How does it compare with other areas in psychology?

Interest in Comparative Psychology

In general, there are a number of reasons for concluding that interest in comparative psychology is holding its own fairly well in relation to other research fields. In the first place, there seems to be an increasing demand for publication outlets in the field. An analysis done, by the writer, of the *Journal of Comparative and Physiological Psychology* from 1948 to 1956 indicates that between these years the number of articles almost tripled. The greatest jump occurred in 1951 when a new editorial policy of publishing more articles of shorter length came into effect. Since this date, the number of articles has increased about 67 per cent in six years. In the second place, two new journals of animal behavior have made their appearance in the last ten years, *Behaviour* and the *British Journal of Animal Behavior.* Like their older counterpart in Germany, *Zeitschrift für Psychologie,* these contain studies both observational and experimental, involving a wide variety of species. Third, numerous symposia have been held on the subject of animal behavior during the past decade, and, as Harlow has pointed out [51], research funds have been going increasingly to the support of animal work.

On the whole, then, there are strong indications that animal research is a vital and growing field in psychology. Granting its vitality as a field, we may further inquire as to its scope. Two major questions will concern us briefly: (*a*) Is it narrow or highly diversified in its theory and choice of problems? (*b*) Does it cover many animal species or only a few? Let us examine each of these points in turn.

The Breadth of the Field. In general, this is difficult to assess. There are very few theories of comparative psychology as such, and, with one possible exception [78], we have nothing that might be called a systematics of behavior in the same sense that biologists have a systematics of morphology. For the most part, animal behavior is studied in an empirical way without particular regard to such broad theorizing. Though narrow from the point of view of theory, it is quite broad in regard to the range of empirical problems. But there is no gainsaying the lack of variety of, indeed, lack of interest in, any theoretical formulations about the comparative aspects of behavior. It is a task for the future to rectify this situation (see Chap. 2).

Range of Species. The second query we have raised is also rather difficult to answer exactly. However, it should be emphasized that it concerns an issue that is of more than merely academic importance. The comparative psychologist has nearly a million different species to choose from. Many of these can be studied in the laboratory, and almost all of them can be observed in nature. Clearly, unless we study many different species, we shall never be quite sure that theories built up on one species will be fully applicable to the behavior of others. This point is well illustrated by the gulf between the theoretical models of the ethologists in Europe and those of learning theorists in America. The former seem to be more applicable to the behavior of birds and fish in a natural setting, while the latter are more useful for describing the behavior of the rat in highly controlled situations. Only by having the same experimenters work with many animal species will there be any possibility of developing a comprehensive theory of animal behavior.

In addition, different animals are especially useful for different problems. The guinea pig, for example, because it happens to have a highly accessible cochlea, is valuable for work on audition; the mouse, because about eighty inbred strains of this species are available, is the most natural choice for the genetically oriented psychologist. The fact that cortical maps have been made for a number of mammals, such as the dog, cat, rabbit, and monkey, make them especially useful for neurophysiological and sensory work.

How broad is the field at present in respect to the number of species studied? Up to 1948, at least, there seems to be little doubt that comparative psychology in America was rather narrow in its scope. Although we have no exact data to indicate this, we can say with some assurance that this narrowness was not nearly so characteristic of European psychology. Indeed, the articles of the European contributors to the Fourth Symposium of the Society for the Study of Experimental Biology in 1949 on physiological mechanisms and animal behavior [122] strongly support this assertion. It is likely that this difference between American and European comparative psychology is due to different historical traditions. In America, the study of animal behavior arose mostly within psychology and was geared, at first, to answer general problems such as learning, thinking, and motivation. It is not surprising that choice of animal subjects should then be dictated by considerations of economy and convenience. In Europe, on the other hand, comparative study of behavior arose mainly from zoology, with its intrinsic interest in animals as such and its orientation to problems of taxonomy and morphology. The natural outcome of such an orientation would be the study of as many different animal species as possible.

Nevertheless, there are strong indications that things are changing on the American scene. The important papers of Schneirla [116], Lorenz [78], and Beach [7] decrying the overuse of the rat in America have not been without their effects. Furthermore, the vigorous ethological movement in Europe has been having a growing impact on the study of animal behavior in this country. American comparative psychology is slowly but surely becoming more interested in studying a greater variety of species. An examination of the *Journal of Comparative and Physiological Psychology* and of the *Psychological Abstracts* between 1948 and 1956 clearly indicates an increasing use of animals other than the rat. It is hoped that this trend will continue.

We may conclude, then, that the general field of comparative psychology shows considerable vitality, that it is tending increasingly to the study of a greater variety of animal species, but that it is still somewhat narrow in its theoretical formulations as comparative psychology.

Let us now turn to the main part of this chapter dealing with trends of research in different areas of comparative psychology. Obviously it is impossible to do justice to such a topic in one chapter. Only the whole text can do this. Nonetheless, we hope to present a quick bird's-eye view of some of the work described in more detail in the previous chapters, pointing up underlying trends and convergences in both theoretical and empirical interests. We have, of course, by necessity, omitted much important work. But if the sample of work presented is only able to whet the appetite of the reader for further reading and research in comparative psychology, it will have served its purpose. In the following sections we shall attempt to describe briefly some of the major lines of research in the various problem areas of comparative psychology. We have arbitrarily chosen six major areas of work for separate consideration. These are: (*a*) sensation and perception, (*b*) drives and motivation, (*c*) learning and cognition, (*d*) emotion and abnormal behavior, (*e*) heredity and environment, (*f*) social behavior. It is fully recognized that other breakdowns could well have been made. The one used here is only one of many possibilities.

SENSATION AND PERCEPTION

Sensation

Chapter 4 of this text has well indicated the mass of information available at present on the sensory modalities of representative species along the phylogenetic scale. As the student will have realized, a great deal more is known about vision, anatomically and functionally, than is known about hearing. Further, more is known about hearing than about the chemical senses, while information on the remaining sensory modalities is extremely meager. This variation in the amount of information is not necessarily paralleled by a decreasing importance of the different sensory modalities in the animal's adjustment to his environment. It probably reflects to a greater extent the unavailability of adequate methods for their study, both methods of stimulation and methods of recording. It may be that the more recent electrophysiological methods being developed by Granit and others [54] will open the way to a fresh approach to the nature of those modalities that do not respond very well to anatomical and behavioral techniques.

On the central and physiological side, more and more studies concerned with exactly defining the cortical sensory pathways have appeared. These studies have made use of electrophysiological techniques (see Morgan and Stellar [93]). We now have a fairly good idea, for example, of the cortical topography of vision, audition, and the other senses in a number of species. This knowledge permits much more exact control in experiments involving the ablation technique. Thus, it has been possible to define the visual areas in the cat much more precisely by these electrical techniques than was previously possible using only standard anatomical methods. As a result, we may now make inferences about the effects of visual-cortical removal on visual functioning (e.g., discrimination) in a much more exact manner than we could previously. The same possibility applies to audition and other modalities [95].

Nonetheless, it must be recognized that we have a great deal more fact than theory. For example, the duplicity theory is given some support, as is shown in Chapter 4, but it may be refuted by discoveries made possible by the use of the electronic microscope and action-potential techniques. Again, the discrepancy between the electrophysiological and the psychological or behavioral data relative to color vision in the cat constitutes an unsolved puzzle. Except in a number of rather limited problem areas, very little has been done from the standpoint of comprehensive theoretical construction, especially within an evolutionary framework. Perhaps the time is now ripe for such a move.

Perception

In practice it is very difficult to separate work on perception proper from work done on complex learning processes. Although there is some justification for treating perception and learning separately, most experimental methods used to study them in animals necessarily confound the two. Thus, as the writer has pointed out elsewhere [129], it is difficult to know, e.g., in pattern discrimination by a rat, what proportion of the trials taken by the animal to reach criterion is spent in actually perceiving the difference between the patterns and what proportion is spent in learning to respond to the correct or rewarded pattern. By using the exploratory rather than the hunger drive as a motivating condition, the writer found that rats show almost immediate or "spontaneous" discrimination between a triangle and striations equated for brightness. It would be interesting to see whether the same applied in the case of more similar patterns. In view of the stress given recently to the study of exploratory behavior, it is not unlikely that this method will be used more and more for studying perception in animals. Perhaps the work that comes closest at the present time is that of the ethologists on the kinds of sign stimuli that release various reactions (see Chap. 3).

Another line of work on perception has recently come into popularity: the relationship of adult perception to early experience. For a long time, through the influence of gestalt psychology, it was believed by many that perception is innately given rather than learned. Riesen's now classic experiments on the effects of early perceptual restriction in primates [109] have clearly indicated that much of perception is actually learned. An animal, reared in darkness, shows very poor visual perception later on. Apparently, according to Nissen, Chow, and Semmes [97], the tactual and kinesthetic modalities are also retarded by analogous restriction in early life. On the basis of this kind of work, Hebb (see Chap. 7) has developed a theory of perceptual learning which takes "unity" of figure as innately given, but *identity* (i.e., particular form properties) as learned by experience. Although, so far, the theory has not been put to exact experimental test, it generally agrees with the data available on the subject.

The Role of Sensation and Perception in Animal Behavior

One of the most interesting aspects of research on sensation and perception involves studying the role of stimuli in releasing or guiding certain kinds of behavior patterns. The behavior of the bat will serve as a good example. Griffin has found that the bat [42], and some species of birds [44], can avoid obstacles in their path as well as locate prey [43] by means of echolocation. As they fly they emit high-frequency sounds that bounce off objects and echo back to them, thus locating the objects in space for the animal. Here is an instance of a sensory mode used in a most ingenious way—much as human beings use sonar—to guide behavior. Echolocation has also been attributed to the rat [111]. Along similar lines, a problem that has interested many investigators is navigation and homing, especially in birds. We know that many bird species are able to fly extraordinary distances to a habitual summer or winter roosting territory without much error. How they can do this is not yet known but has been a subject of theory and experiment for some years. Until recently, navigation tended to be explained in terms of magnetic and Coriolis forces, some investigators [11] suggesting anatomical bases for such responses in the vestibular sense organs. These ideas have lately given way to sun-navigation theories [72, 84] that stress visual responses to the position of the sun which synchronize or do not synchronize with an internal clock, thus telling the animal his approximate location and distance from home. This explanation seems to require an inordinate sensitivity on the part of the avian eye, and it is for that reason that Pratt [104] has gone so far as to suggest that some extrasensory factors are involved. In fact, as Thorpe has pointed out [130], bird vision is very acute and can probably handle such complex perceptual tasks. Obviously, the problem is still not completely solved. Many factors must be involved, and these may well vary with different species. Carthy [22, 23] finds, for example, that one species of ant tends to use polarized light for orienting, while another species is guided mainly by odors. Furthermore, homing and navigation both may depend to an extent on experiential factors. Matthews [85] has shown that young, untrained pigeons will orient to a home loft fairly accurately, though they home poorly, thus implying that some practice is necessary. At the present time, much work is being done on this subject, and before long we may expect that at least some of the difficulties will be cleared up.

DRIVES AND MOTIVATION

The general topic of motivation has been assuming more and more importance as a topic of systematic enquiry in psychology. Motivation is, of course, a very old construct, with origins going back before the present century. Nevertheless, there is a strong indication from books, articles, and symposia that it has come to occupy a much more central and independent status today. More work is, in fact, being done than can be described in this volume, even in the broad outlines presented in Chapters 5 and 6. In this section we shall confine ourselves to pointing up a few trends in research on drive and motivation that appear to be particularly interesting and vital.

The Physiological Basis of Drive and Motivation

New answers are appearing to an old problem: how are hunger, thirst, and other drive conditions "registered" on the central nervous system? Ever since the early reports of Cannon [20] and Richter [108], a great deal of work has been devoted to the exploration of physiological and homeostatic aspects of drive states such as hunger, thirst, and sexuality. At the time, this work represented, as Harlow [50] has pointed out, a swing away from an interest in the external to the internal determinants of behavior. Although there are many indications, as summarized in Chapter 6, that the pendulum is swinging back again to an interest in exteroceptive motivation, it is still true that the study of biological drives is a popular one today. The "local" theories suggested by Cannon [20] to explain hunger and thirst have, of course, been revised and modified in the light of experimental evidence. Today, workers in this area are leaning more and more toward complex explanations in terms of biochemical changes [93]. It is becoming increasingly clear that a sound knowledge of biochemistry is a prerequisite for work in this area and that just as psychogenetics became a definite field in the behavioral sciences, so will "psychopharmacology" become one. A good account of the kind of work that can and has been done is given by Beach in *Hormones and Behavior* [6]. Indeed, the experimental work of Beach and his associates at Yale and of W. C. Young and his associates at Kansas on the sexual drive serves as an excellent prototype. It is of considerable interest and importance to our discussion of research trends that both these groups have related the development of mature sexual behavior both to genetic and experiential factors. Thus Valenstein, Riss, and Young [133, 134] find that an organized pattern of intromission and ejaculation in the guinea pig depends on social experience with other animals during development, and this dependence itself is somewhat related to genetic-strain differences. Beach [5] has previously reported similar findings.

As indicated in Chapter 5, Biological Approach to Motivation, a neurological model for motivation is now available. Stellar [121], in an excellent review, takes as his starting points Morgan's concept of *central motive state* (CMS) and the experimental work of such men as Ranson, Bard, Kleitman, Hess, and many others. He develops a neurological theory that links motivation closely to hypothalamic centers, these being influenced both by internal (e.g., hormonal) and external (e.g., environmental) factors. Among other advantages, Stellar's theory brings together under one framework a number of different kinds of motivation that have been studied separately in the past, such as sex, sleep, hunger, thirst, and emotion. Further, it is a multifactor theory which can encompass all the many facets of motivation, and it includes both peripheral and central, experiential and innate determinants. A somewhat different neurological approach to the problem of drive has been suggested by Hebb [59], who proposes that the energic aspects of drive be attributed to the generalized activating system originating in the brain stem.

So far, neither of these theoretical approaches has been fully tested. Certainly both seem capable of generating fruitful empirical hypotheses. For example, Hebb's stress on the necessity for an arousal component in motivation and on the fact that organisms often seem to seek stimulation rather than to avoid it is supported by the interesting findings of Olds [100, 101]. This investigator found that rats will learn instrumental acts in order to obtain stimulation through electrodes implanted in certain areas of the midbrain. This line of research, now being continued in several centers, is a most important one and represents a definite research trend in the physiological study of motivation in animals. Furthermore, it is of interest to note that it has been extended along biochemical lines. Olds [102] has now developed a *self-injection* technique by which the animal's tendency to seek central stimulation by various chemicals can also be studied.

External Determinants of Motivation

Chapter 6 reviews the increasing number of studies of motivation as controlled by external or environmental factors. This kind of emphasis in the study of motivation has been, until quite recently, rather foreign to American comparative psychology, which has tended to be concerned with internal factors. There are now strong indications of a shift.

In general, the study of exploratory drive involves behavior that is released or determined by the external stimuli encountered by an animal and, in this respect, may follow the same kinds of laws followed by such drives as courtship, aggression, and others with which ethology has been concerned. One of the more striking aspects of the study of exploratory behavior is the great diversity of its origins. Research bearing on it has arisen from work in at least five different areas. Thus, the studies of Montgomery on spontaneous alternation [91] and his finding that this phenomenon could not altogether be explained by reference to Hull's concept of inhibition, led him to postulate an exploratory drive. Latent-learning studies represent another source, as does recent work by Miller and his associates at Yale on secondary approach drives [94]. Yet another of its origins lies in the work on complex learning in primates. Harlow and his colleagues at the University of Wisconsin [53] were, in fact, among the first to realize that primates often like to solve a problem just for its own sake rather than for some extrinsic reward. They have since contributed a great deal of useful information on the subject. In addition, Harlow has given, in a challenging paper [50], special theoretical emphasis to the study of nontissue needs. It seems evident that his plea for more research in this area has not been wasted.

Whether it will turn out that exploratory drive is more like the standard homeostatic drives, as Berlyne [12], Myers and Miller [94], and others have implied or more like some of the nonhomeostatic drives studied by the ethologists, as Harlow has suggested [50], we cannot say at present. There is some evidence recently obtained by Charlesworth and Thompson [24] indicating that amount of exploration is not greatly affected by periods of deprivation between three and nine days. In this respect, it appears to be different from such drives as hunger and thirst. On the other hand, Butler [19] has obtained different results with monkeys. Any final conclusion must await further evidence.

On the more theoretical side, strong impetus was given to this area of research by Hebb's book, *Organization of Behavior* [57]. Hebb's stress on the apparent tendency of organisms deliberately to seek stimulation was undoubtedly instrumental in influencing such work as that of Berlyne on curiosity in human beings and animals [12, 13, 14, 15], that of Thompson and Solomon [129] on spontaneous exploration of visual patterns in rats, and Havelka [55] and Hebb and Mahut [60] on so-called "problem-seeking" tendencies in rats. Since the reader will have encountered many of these experiments in other chapters of this book, we shall not discuss them here in detail. We need only emphasize that there has been a rather definite convergence of interests that may well set the tone of animal research for some time to come. As we have already stated above, work on curiosity and exploratory behavior is now flourishing. Many experimental reports have been and are being published, and we have, in addition, a number of useful theoretical papers on the subject [15, 30, 39].

Motivation as Acquired

Since we shall consider the nature-nurture controversy in more detail in another section, we shall only touch on it here. The main point to be emphasized is that in recent years much work has been directed at discovering some of the experiential determinants of motivation and drive. We have already mentioned above that sexual behavior, for example, depends for its full development upon social experience. Other so-called "primary drives" also appear to do so. Birch [110], for example, has found that adequate maternal behavior in the rat, or at least the components of nest building and licking and retrieving the young, do not appear in the primiparous female unless it has had the opportunity to manipulate movable objects in the environment and lick itself previous to littering. The complex sequence of behavior involved in the maternal drive is clearly not innate in the usual sense of the term but depends heavily on experiential factors. According to Hebb [57], hunger is no exception to this rule. Apparently, an animal learns hunger and the appropriate responses to it.

On the more ethological side, we find similar instances. Beach [7] cites the case of a moth which normally lays its eggs on hackberry leaves in preference to any other kind of leaves. This preference appears regularly in each generation. However, if eggs are transferred to apple leaves, the situation changes. Many of the females which spent their larval stage on apple leaves now prefer to lay their eggs on these rather than on hackberry leaves. In such a case as this, the traditional dichotomy between innate and learned obviously breaks down. Almost all types of motivated behavior appear to depend on experience. It is a welcome sign that workers in the field now recognize this fact and are opening up new and interesting lines of research in order to explore its ramifications more fully.

A second important area of related research concerns the manner in which secondary drives are acquired and their relationship to instrumental learning [88, 120]. As indicated in Chapter 6, animals can acquire fear or anxiety which can serve as a drive motivating many types of behavior. Although work on this problem has not so far been extended in this direction, it is possible that it may well contribute to our understanding of the complex kinds of motivations that we have discussed above. Maternal behavior, for example, seems to be, in some sense, an acquired drive. It would be interesting to know whether the same kinds of principles used to describe the acquisition of a fear drive could also be used for maternal drive.

LEARNING AND COGNITION

Clearly this area has been, and still is, one of the major fields of interest for psychologists working with animals, particularly in America. Between 1951 and 1956 more articles on animal learning appeared in the *Psychological Abstracts* than on any other subject. At the same time, the theoretical models they have introduced into psychology, while enormously useful in terms of the research they have generated, have tended to cast American comparative psychology into a rather narrow mold. Not only have we been inclined to use only a few kinds of animals in this country, we have also tended to stick to a limited number of somewhat oversimplified methods and principles to study and to explain learning. Much the same may be said of the U.S.S.R., where a rather doctrinaire Pavlovianism [119] has prevented development in many directions. In Europe and England, on the other hand, psychologists have tended either to follow American leads in the study of learning or else have preferred to deal with other topics. However, signs are appearing of some *rapprochement* between ethology and American learning theory, some of which we have discussed already. To develop this general point of view, we shall now consider the general topic of animal learning under several subheadings.

Simple Learning

One of the most interesting findings made by ethologists with regard to learning has had to do with the phenomenon of *imprinting*, first reported by Heinroth [62] and later taken up by Lorenz and others. Imprinting refers to a simple, relatively irreversible learning that occurs in some species during a short period in early life. Heinroth found that young geese, reared from the egg in isolation, learn very quickly to follow their human keepers as they normally would their mother. Apparently they react, within a few hours after hatching, to the first large moving object they see and attach themselves to it tenaciously. These original observations on imprinting have now been extended and verified by many workers [130]. Imprinting is of interest for several reasons. In the first place, it represents a kind of basic learning that has not been systematically studied before and one that is somewhat unlike any other. In the second place, it points up the "acquired" aspect of many supposedly innate kinds of behavior. In the third place, on the theoretical side, it represents a natural point of contact between the ethological and the American learning-theory tradition. Most comparative psychologists have not been slow to recognize these points. As a result, we find in America a growing interest in the laboratory study of imprinting, well exemplified by the studies of Ramsay and Hess [105] and Jaynes [68, 69]. These experiments have involved exposing the young animal to objects of varying sizes, shapes, and colors for varying lengths of time at different periods of development. In this way some of the main dimensions of the phenomenon can be discovered. For example, Hess [63] reports in one experiment that strength of imprinting varies not so much with the length of exposure time to the object but rather with the amount of effort expended by the young animal to get to or to keep up with it.

While there has been a growing tendency for American workers to study ethological material, there also has been an increasing tendency for ethological workers to make use of some of the theoretical constructs developed by learning theorists in America. A good example of this can be seen in the work of Hinde [64] on the mobbing behavior of the finch. Specifically, he has attempted to relate the habituation of the mobbing response to live and stuffed owls to Hull's two-factor theory of extinction (reactive inhibition and conditioned inhibition). Certainly, his data seem to indicate the operation of a short-term and a long-term response decrement that can aptly be described in Hullian terms. Thorpe [130] has reviewed similar observations and has elaborated in more detail their theoretical possibilities along these lines.

In addition to the two foci of interest that have been highlighted above, there also exists a large and relatively unsystematized body of information on the learning of many species in many different situations, some natural and some laboratory. Several good reviews of this work are available [96, 98, 130], and we have the useful periodical accounts to be found in the *Annual Review of Psychology* in America, as well as *L'Année psychologie* in France, among others. On the whole, it is fairly clear that rat learning in America, and dog conditioning in Russia still dominate the over-all research scene. Hull and Pavlov have, without a doubt, had a tremendous influence on psychology in the two countries and probably will continue to do so for some time to come.

At the same time, however, the dog and the rat are not the only animals being studied. A number of most interesting papers have appeared on learning in animals belonging to lower biological groups. Perhaps this is nothing very new to comparative psychology. This kind of work does indeed have a long history. At the same time, it is worth stressing, if only to show that such work has not died out. A good example of it is the work of Beatrice Gelber [37] on learning in *Paramecia aurelia.* She has shown that many individuals in a colony of these small organisms can become positively conditioned to a sterile needle, if they are initially exposed for a number of trials to the needle baited with nonmotile bacteria. The index of learning consists of a count of the number of animals in the experimental group found clinging to the needle in a test trial with food absent, as compared with a count of animals from a control group. Not everyone, however, has agreed that this adequately demonstrates learning in *Paramecia.* In a recent report, Jensen [70] has shown that Gelber's training procedure creates localized pools of bacteria-rich culture fluid in which the animals tend to congregate before the appearance of the sterile needle. Further, the presence of bacteria, as opposed to their absence, promotes the attachment tendencies, or thigmotropic responses, of *Paramecia.* Consequently, it is not safe to conclude that learning occurs in these organisms. We cannot, of course, say that it definitely does not occur but merely that the evidence so far does not completely support such a hypothesis.

Another related series of experiments on lower organisms has been that by Lepley and Rice [74] on *Paramecia* and by Grosslight and Tichnor [45] on the meal worm, *Tenebrio molitor.* These studies seemed to indicate that the behavior of the subjects conformed to Hull's principle of reactive inhibition. Both *Paramecia* and meal worms, like mammals, tend to avoid repeating a reaction just made, such as a right or left turn in a T maze. In addition, as has been found with rats, this tendency varies inversely with the length of the path between the forced turn and the subsequent free one.

Since our aim in this chapter is only to summarize, we shall not multiply examples. We merely wish to emphasize that studies of this kind represent a valuable contribution to the comparative psychology of learning and that we need more like them. Let us now turn to the work concerned with "complex" learning.

Complex Learning

Although the rat can be trained to perform acts of a considerable degree of complexity, it is doubtful if it can really compete with the lower primates in this respect. In recent years, as a result of the growing popularity of monkeys and apes as subjects in experiments, there has been a definite swing in the direction of studying more and more complex learning. We now have a quite massive collection of data, coming from such institutions as the primate laboratories at Wisconsin and Orange Park, showing that these animals can be taught to solve very difficult problems, sometimes involving the manipulation of several dimensions at the same time. So far, most of this work has been quite empirical and not particularly related to any theoretical model. One of the most important developments to come out of it has been concerned with learning sets or "learning to learn." Explanations of learning sets pose a difficult problem for most standard theoretical models of learning. Indeed, it is likely that new kinds of models will have to be evolved if we are to understand this sort of learning adequately. It is probable that these will not be long in forthcoming, since the study of complex learning and learning sets has been extended to many other species (see Chap. 7).

Learning and Motivation

Although we have discussed motivation in a previous section, we must necessarily return to it at this point to emphasize an important trend in the work relating it to learning. Since Cannon, it has been for many theorists a primary principle that behavior is always geared to the restoration of equilibrium [66] or to the reduction of drive stimulation [88] and that if these do not occur, no learning takes place. It is now becoming clear that animals will often behave in such a way as to increase stimulation and in fact, will show definite learning when an increase in stimulation is offered as a reward (see Chaps. 5 and 6). Many examples could be given to establish this point: animals do not always seek to diminish tension, and accordingly, it is a mistake to equate need satisfaction with need reduction [99]. There is a growing realization of this fact reflected in a large number of theoretical and experimental papers.

Phylogeny of Animal Learning

With very few exceptions, most workers in the field have come to regard the task of establishing a phylogeny of learning as an enormously complex one [96]. Evolution has not produced a single series of animal groups, neatly gradated in ability and complexity, but rather a large number of lines, some parallel, some converging, and some diverging. Furthermore, learning problems that might be appropriate for one species are quite unsuitable for another, as Fuller and Scott [34] have pointed out. Thus the series of experiments on delayed response in about nine different species, collated and reviewed by Maier and Schneirla [83], does not really give us very much information about the evolution of learning, though it is nonetheless valuable in other ways. Maier and Schneirla, of course, clearly recognized this. The fact that, under certain conditions, the rat can show delays as long as those shown by monkeys and apes might well seem surprising from a zoological point of view. For that matter, the wasp (*Ammophila campestria*) is almost as good, showing delays up to 15 hours [131].

Tinbergen has clearly pointed out the moral to be drawn from the failure of such comparisons: "In view of the differences between any one species and another, the only thing that can be said for certain is that one should *not* use identical experimental techniques to compare two species, because they would almost certainly not be the same to *them*" [131, p. 12].

At the same time, while crude comparisons between species may be fruitless, comparisons that are made with some definite hypothesis in mind may often yield valuable information. Fink [31], for example, has recently compared the performance on an arrow maze of man, pig, dog, goat, rat, chicken, rabbit, cat, and a selection of water turtles and land tortoises. Whatever we may think of his measure of performance, at least he has a rationale for it, namely, that it employs only the "animal's natural means of locomotion" and therefore taps a basic ability that is not specific to any particular species. One may not agree with this point of view, but at least it is as sensible as analogous attempts at the human level to find "culture-free" tests.

From a biological standpoint, the approach of Rensch [106] to the phylogeny of learning ability has been more sophisticated. Taking the hypothesis that intelligence correlates with brain size, he has compared the performance of a number of animals of varying brain mass, for example, the mouse, the rat, and the elephant. As far as they go, his experiments appear to support his theoretical viewpoint on the phylogeny of learning.

One of the most elegant phyletic analyses of learning worked out so far has been that of Harlow [52] on various monkey and ape groups in the primate order. This work is sound both from the zoological and from the psychological point of view. In contrast to most researchers in this area, Harlow used a logical evolutionary series which included animals of rather similar physical characteristics and a proven and well-worked-out method of measuring complex-learning ability—the learning-set method. It is of great interest that the ability of the various groups to develop learning sets corresponded closely to their evolutionary position within the primate order.

The difficulty with this kind of work, of course, is that it requires rather extensive facilities—more extensive than those usually available to most investigators. Consequently, for the time being at least, comparative psychology will have to be content with the hope that the efforts of many private investigators working on different species can eventually be fitted into some coherent evolutionary framework. Obviously, such a task can only be feasible if there is some comparability among the work of all the individuals involved. At the present time, unfortunately, there is more disagreement than agreement. Perhaps some of the attempts that are now being made at *rapprochement* between the American and European schools will do something to rectify this situation.

EMOTION AND ABNORMAL BEHAVIOR

General Studies of Emotionality

A perennial problem in the study of emotion in animals has been that concerned with methods of measurement. In this respect, American workers have in their descriptions of emotion lagged far behind European ethologists. In the rat, for example, one of the most common measures used has been incidence of urination and defecation [47], although, as it turns out, these indexes have limited generality [17]. What is needed is a more exact naturalistic description of behavior in a situation that is known to be stressful. Very few people have ventured in this direction, although there are some notable exceptions. Thus, Melzack [86], extending the ideas of Hebb [56] on so-called "irrational fears" in animals, has examined qualitative differences in the emotional responses of dogs to various "strange" but innocuous objects, such as a skull, an opening umbrella, a balloon being blown up, and many others. The different objects produce varying amounts of avoidance or aggressive responses, much as they do with chimpanzees. It is interesting, as Melzack points out, that the differential responsiveness of the subjects clearly indicates that the dog can make immediate and spontaneous discriminations of visual patterns in three dimensions. As in the case of the rat [129], this fact is usually not obvious when conventional testing methods are used. In another paper, Melzack [87] finds further that early restriction adversely affects the selectivity of emotional response, leaving mainly a diffuse excitement. This general approach to the problem of emotion is undoubtedly a fruitful one and deserves to be followed up. The observations of animal emotion made many years ago by men like Darwin [28] and Romanes [112] may have been overly picturesque, but they probably had more potential value than the rather sterile, single-response measure used today.

Along more theoretical lines, Thompson and Higgins [128] have attempted experimentally to cast some light on the question of whether emotion is organizing or disorganizing (the Leeper-Young controversy). It was found that rats that are shocked at a choice point of a modified T maze tend to go to the side to which they have previously been habituated rather than choose in a random or disorganized way. Nonshocked animals, on the other hand, prefer to go to the new and unfamiliar side. Several qualitative indexes of rat behavior used supported the general conclusion that under the experimental conditions employed, emotion had an organizing rather than a disorganizing effect.

A quantity of material is now available on the physiological and neuronal basis of emotion. Thanks to the work of such researchers as Bard and Mountcastle [4], we are now beginning to know just what parts of the brain are involved in emotion. Clearly, these are more numerous and complex than previous workers thought, some of them appearing to have excitatory and others inhibitory functions. On the more peripheral side, an interesting attempt was made by Royce to describe the basic physiological and psychological dimensions of emotionality in the dog by means of factor-analytic techniques [114]. Using fifty-three pedigreed dogs of six different breeds, Royce intercorrelated scores made by the animals on thirty-two different physiological and psychological variables. Ten factors were extracted by means of Thurstone's centroid method. Rotation to simple structure yielded ten factors: timidity, heart reactivity, aggressiveness, activity-level, audiogenic reactivity, and a second timidity factor, plus four others which were undetermined and not interpreted. This kind of work should do much to help solve one of the basic problems in behavior—namely, finding units of behavior that can be manipulated either experimentally or genetically. Certainly, if factor analysis could somehow be combined with ethological description, some useful information might well result.

Effect of Stressful Agents

As indicated in Chapter 10, a considerable amount of work has centered around the nature and etiology of convulsive behavior in the rat. Starting in the 1940s, largely with the work of Maier [80], a great deal of energy was expended by researchers in many laboratories to explore all possible ramifications of sound-produced seizures in the rat. Although Maier originally regarded this behavior as "neurotic" and initiated by conflict, most workers have come to the view that while intense sound is both a necessary and sufficient condition for convulsions, conflict is neither. As Bevan has pointed out in a review of all the audiogenic-seizure work [16], a number of important lines of research have arisen from this work. It has had considerable usefulness, both as a problem to study and as a technique to use in other connections. Among these, it seems to the writer, one of the most important uses relates to the examination of the genetic transmission of seizure susceptibility [35, 38, 48]. Because of its all-or-none character, the sound-produced convulsion represents a behavioral trait whose inheritance is much easier to study than other traits such as intelligence, emotionality, or activity, although it may have less intrinsic interest than these. If only serving as a means for setting up models of the genetics of behavior and thus giving impetus to the study of psychogenetics, the audiogenic seizure is a phenomenon whose study has definitely paid its way. It is significant that while many of the other lines of research in this area have all but disappeared from the literature, the study of seizure inheritance is still studied in a number of laboratories.

Another line of work, somewhat related to that described above, is that on the effects of electroconvulsive shock on behavior. Its effects on learning are so complex and dependent on such a large number of factors [115] that we cannot discuss them at length here. One clear-cut example, however, is its effects on emotional conditioning in a Skinner box. In a long series of careful experiments, Brady and his colleagues (see Chap. 12) have shown that ECS can eliminate emotional conditioning. While rats that have not had ECS stop bar pressing for food at the onset of the CS, shocked rats do not, but continue pressing. The effect does not occur if the seizure is suppressed by drugs. This interesting result suggests a possible mechanism for the therapeutic effects of ECS in human beings.

In addition to ECS, other agents have also been arousing interest, some of these, like X irradiation [2, 36], having a somewhat topical importance, others, like various chemicals, having more basic significance. Indeed, as we have already pointed out, there are many signs that an interest in the biochemistry of behavior is developing strongly.

One last point must be mentioned in this connection. The work described has been concerned with the psychological effects of stress. Inasmuch as there has been in medicine a strong interest in the physiological effects of stress, arising largely from the work of Selye [118], psychological research in this area is of prime importance. Indeed, several attempts have already been made to point up applications of Selye's theorizing on stress to behavioral phenomena [18, 138]. It is likely that this area will fast become a focus of great activity in animal psychology.

Neurotic Behavior and Conflict

Much of the newer as well as the older literature on neurotic behavior in animals has been reviewed in Chapter 10. A great deal of the material relates to the Pavlovian kind of study of conflict, while some of it is concerned with later developments, such as those relating to current learning theory. It is these latter that appear to represent a real trend in the study of neurotic and abnormal behavior.

One of the more promising of these lines of research has stemmed from Miller's experimental studies of approach-avoidance conflicts in the rat

[89]. As outlined in Chapter 10, the degree to which an animal will approach a goal is expressed as a function of both the positivity and negativity of the goal. Strength of avoidance diminishes (i.e., generalizes) rather sharply, and approach rather gradually, with distance from the goal. Thus vacillation will occur at a distance from the goal that is given by the point of intersection of the two curves. If both approach and avoidance tendencies are strong, the animal will vacillate at a point quite close to the goal but show high anxiety according to prediction. On the other hand, if both tendencies are rather weak, the animal may also stop rather close to the goal and show only low anxiety. Most of the basic predictions generated by this model have been experimentally tested and seem to stand up well. Interesting applications have been made both to psychotherapy and to projective test behavior in human beings [40, 89] and, of more importance in the present context, to exploratory behavior [92]. In addition, although this has not so far been attempted in any detail, the model should prove to be very useful for ethological studies. The work of Hinde [64] on the "mobbing" responses of the finch to predators (real owls and wooden models) serves as a good example. If an owl or owl model is placed outside the cage of a chaffinch, it will make mobbing flights both to the front and to the back of its cage. The proportion made in each direction varies not only with the distance of the owl from the cage but also with the authenticity of the model. This is clearly a conflict situation involving both positive and negative components, as Hinde points out, and might well be analyzed in terms of Miller's model.

Another aspect of neurotic behavior in animals that has interested many researchers has been the so-called "abnormal fixation," originally described by Maier and his associates [81]. When forced to try to solve an insoluble problem, rats often develop highly stereotyped responses which, according to Maier and Ellen [82], do not appear to be describable in terms of current learning theory. Both Wolpe [139] and Knöpfelmacher [71], among others, have disagreed with Maier's interpretation and, in experimental tests, were unable to confirm deductions made from his "frustration" theory. Interest in this topic is currently fairly strong.

Miscellaneous Studies of Abnormal Behavior

There have appeared in the literature a number of studies which cannot be said to reflect any basic trend but which are nevertheless interesting and suggest new lines of work. Of these, we shall only mention a few. Ullman [132] has found that "compulsive eating symptoms" can be experimentally produced in rats if hungry animals are shocked while eating. Little training in eating, strong hunger, and strong shock appear to be the conditions most conducive to the development of the symptom. Generally speaking, it would seem that his results might also be amenable to treatment by Miller's conflict model. In another experiment, Datel and Seward [29] studied a response in the rat rather analogous to Ullman's compulsive eating. This was a persistent ear-scratching response. According to these workers, ear scratching which is initiated by application of collodion will continue some time after the effects of this agent have worn off. They interpret this result in terms of the Hullian principles of secondary motivation and reinforcement. It is possible that many psychosomatic symptoms could be profitably studied in this way. Somewhat similar is the experimental report of Mahl [79] on the production of ulceration in dogs by conditioning chronic fear in response to shock. It is of great interest that gastric acidity was found to increase even when the primary stimulation of shock was omitted. This illustrates very well the strength and persistence of anxiety as an acquired drive.

In view of the excellence of some of the work that is being done, it seems likely that both Pavlov [103] and Beach [8] were justified in expressing the hope that animal studies would eventually contribute a great deal to our understanding of human emotion and psychopathology.

HEREDITY AND ENVIRONMENT

The study of the inheritance of behavior has had a long if spotty history in psychology. As general orientation has shifted from nativism to environmentalism and back again, so the number of experimental studies and theoretical papers on inheritance have fluctuated. Although the influence of Watson [137], Kuo [73], and others who tried to construct a psychology without heredity was great, it has never been able to sway psychologists completely away from the study of heredity. Today most students of behavior are willing to admit that behavior does ultimately come under genetic control and that this aspect of it may be legitimately studied. Perhaps two events were most influential in setting an intellectual climate favorable to this point of view: first, the institution at the Jackson Memorial Laboratory, Bar Harbor, Maine, of a large-scale program of research on behavior inheritance; and second, the publication of Hall's article on psychogenetics in *Handbook of Experimental Psychology* [49]. The work on innate behavior of the ethologists should also be mentioned as contributing to the point of view. Since then, it is fair to say that work in the area has been flourishing, as we shall attempt to show shortly in more detail.

It may perhaps seem curious that the study of environmental influences, that is, nonheritable causative factors, should also have become very popular simultaneously. However, it is really not so surprising when one remembers that heredity and environment are complementaries rather than opposites and that consideration of one inevitably involves a consideration of the other. Thus, the two lines of work can, to a great extent, be traced to the same origins. At the same time, in addition to the stress laid on environmental as opposed to heredity factors, there has also been a stress on early as opposed to later environment. The origins of this latter research trend are somewhat different. They revert chiefly to the work of Christie [25], Riesen [109], Hebb [57], and others, all of whom have felt that what happens to an organism in early life is much more important for the organism's behavior than what happens later in development.

This work has been so well covered in Chapter 11 that no review of the techniques, problems, and results on lower vertebrates is needed here. Dealing with the other end of the scale has been the recent work of Hirsch and Tryon [65] on *Drosophila*. They have suggested a method called "mass screening" by which behavioral traits may be reliably studied in these animals as a prelude to genetic analysis. Since so much is already known about the make-up of *Drosophila* chromosomes, this species should prove to be a most valuable subject for psychogenetic experiments.

Since systematic research in this area is now gaining some headway, we may expect that, before long, we shall know much more about the genetic mode of transmission of psychological traits than we do now. Certainly, our present knowledge is meager and inconsistent. One of the chief difficulties has arisen from the fact that most psychological characters are so complex that they cannot possibly have any simple genetic basis. Until we can find some way of getting "units" of behavior, it is unlikely that we shall achieve any great degree of success in the field of psychological genetics. It is a good sign that investigators in the area are quite well aware of this basic problem and have attacked it both along empirical [1] and theoretical [126] lines.

Early Environmental Effects on Behavior

In the last decade, we have obtained a great deal of information about the effects of early environment on later behavior [10, 123]. Perhaps the event most influential in starting this line of work was the publication of Hebb's *Organization of Behavior* which strongly emphasized this period of development. Starting mostly in the 1950s, this work has followed a number of different lines. One of the most popular has involved the study of the effects of restriction in early life on later behavior. Results of these experiments (done mostly on dogs and rats) show clearly that lack of environmental stimulation during the first phases of development can cause serious deficits in such types of behavior as perception [109], intelligence [32, 67, 123], activity-level and motor coordination, emotionality, and social behavior [123]. Conversely, another series of experiments has shown that early stimulation, in the form of "gentling" or handling [138] or even mild electric shock [75], is beneficial to rats, in the sense that stimulated animals show more weight gains during development and are more resistant to stress in later life than nonhandled animals. It seems likely, of course, that excessive stimulation will have the opposite effects. This appears to be the case not only when the stimulation occurs in early postnatal life but also when it occurs in prenatal life [124]. Mother rats that have undergone conditioned anxiety during pregnancy produce offspring that appear to be more emotional than control animals. Since these results are based only on preliminary experimentation, they cannot, of course, be regarded as completely conclusive.

The theoretical side of the problem of early environmental influence has so far not been explored much. Some writers have leaned to biochemical explanations [41, 90], while others have attempted to relate the empirical findings in this area to motivation theory [125]. But we still have all too few testable hypotheses to guide research.

The Nature-nurture Issue

Before leaving this section, it may be wise to make a few remarks about the so-called "nature-nurture" problem. Although this issue has been committed to the grave many times, it is still continually being resurrected and reexamined. It may be dead, but it "won't lie down." In the last few years, it has been tackled again by Hebb [58], Beach [9], and Verplanck [135], among others. Obviously, as we have already stated above, it is impossible to describe any behavior as completely innate or completely learned. Hebb has rightly pointed out that, under certain conditions, either environment or heredity may determine all the variance of a character, rather than so much of one and so much of the other. If we fully recognize and accept this point, then we may find that the nature-nurture problem is not something to argue about but rather, as Hess [63] has suggested, an area to be explored empirically. The work of Birch on maternal behavior in the rat, described in Chapter 3, is a good example of what can be done.

SOCIAL BEHAVIOR

Work in this area has increased during the past six years and gives promise of continuing. It is, however, difficult to spot any new major trends, trends distinctive to the study of social behavior, in either theory or methodology. Most recent research has been along fairly conventional lines, although there are a number of exceptions, as Chapter 9 has shown.

General Field Studies of Social Behavior in Animals

For a long time, field observations of animal societies have been the most valuable way of getting information about social behavior. The classic studies, those by Schneirla on the army ant, by Zuckermann and Carpenter on primate societies, by Darling on the red deer, by Von Frisch on bees, and many summarized in Chapter 9 have given us a wealth of information. Two other examples of this kind of work that have appeared more recently are the studies of mule deer by Linsdale and Tomich [77] and of howling monkeys by Collias and Southwick [26]. All of these offer good illustrations of what can be done away from a laboratory setting, i.e., observed behavior of the species is described in terms of dominance hierarchies, cooperation, territory, and population density.

A different approach is offered by the classification of social behavior as presented by Scott in Chapter 9 and by the ethologists; they represent the beginning of a more fundamental analysis of social behavior. This approach should certainly not be ignored by anyone interested in social behavior, especially since it represents a useful liaison between the field and the laboratory.

Special Aspects of Social Behavior in Animals

An important problem arising out of the work on dominance concerns interindividual recognition in the group. Obviously, if stable hierarchies are to exist, individuals must be able to react to each other as individuals and remember which individual is which. Guhl and Ortman [46] have recently examined this problem experimentally. They found that, while multiple factors determined hierarchy stability in chickens, cues connected with the head were most important. Alteration of such cues produced shifts in dominance order. Ribbands [107], among others, has examined the same problem in bees.

The topics of communication and cooperation have also received a good deal of attention in laboratory experiments as well as in field observations. Such classic experiments as those of Crawford [27] have suggested that true cooperation may occur in primates other than man, though this conclusion has not met with agreement in all quarters. Some of the evidence has been summarized and discussed recently by Hebb and Thompson [61]. In the last few years, not much has been done in the way of experimentation on cooperation. Researchers have perhaps come to realize that it is almost impossible to prove that it occurs in lower animals in the same way as it does in man. More relevant are some of the ethological studies that simply describe the organized sequences of responses which occur between animals without attempting to label these sequences as "cooperative" or "noncooperative." The fact that animals do show systematic communication is more significant than anthropomorphic speculation on whether such communication is similar to human social behavior and whether it is conscious or unconscious.

In the social insects, in particular, we are accumulating more and more information since the pioneer work of Von Frisch [136]. Some recent work by Lindauer [76], for example, indicates that swarming bees apparently choose a permanent home by strict democratic procedures. Scouts go out from the swarm to look for suitable sites. When they return, they indicate to the rest of the bees the location they have chosen. As more scouts go out and come back, a majority preference for a particular spot gradually emerges. On this basis the swarm chooses the "best" location, as determined by majority rule. Thanks to painstaking observation and to the application of experimental methods, we are now beginning to grasp some of the basic dimensions involved in the social behavior of animals.

A great deal of interesting laboratory work on social behavior in dogs and mice, coming from the Jackson Memorial Laboratory in Bar Harbor, Maine, is presented in earlier chapters.

We may also mention experimentation on the effects of brain ablations of various kinds on social behavior. A good example is the work of Rosvold, Mirsky, and Pribram [113]. These investigators found drastic changes in the dominance hierarchy of a group of rhesus monkeys as a result of bilateral ablations of the amygdaloid nuclei. In view of the close relationship these centers have to emotional behavior, including aggression, the results obtained make sense. They have been confirmed and extended more recently by Fuller, Rosvold, and Pribram [33], using three breeds of dog. They found effects on dominance, as well as on cognitive behavior, measured by a delayed-response, a discrimination, and a spatial-orientation test. It is interesting that temporal-lobe lesions (including the amygdaloid complex) have effects rather like early restriction, inasmuch as they produce animals which are apparently noncompetitive.

Theoretical Analyses of Social Behavior in Animals

As we have already remarked above, not many useful theoretical models have yet been evolved to describe and predict the social behavior of animals. Both Carpenter [21] and Scott [117] have suggested categories of social behavior that seem to have observational value. Whether these categories are definitive or not, there seems little question that something of this kind is needed to help us describe accurately the social behavior of animals. The writer [127] has attempted to formulate a similar descriptive model, transposing to the level of lower animals the methods used by Bales and his colleagues [3] in their "interaction-process analysis" studies with human beings engaged in group problem solving. The categories involved seem to work fairly well with human subjects, though, of course, this is not to say they would be equally successful for animals. Hebb [61] has found a similar scheme to be useful for understanding the social-emotional behavior of chimps.

SUMMARY

We shall now attempt to summarize and assess the material presented above with a view to describing main trends as broadly as possible in choice of research topics and research methods. In doing this, we shall have regard not only for total output of work but also for increments in output over the last few years. Both are important in assessing trends.

In the first place, we may draw comparisons among the six main areas with which we have dealt in the previous sections. Clearly, as far as volume is concerned, learning and motivation appear to be leading the field in popularity. Social behavior is probably the least popular, while the other three—emotion, sensation and perception, and heredity and environment—fit somewhere in between. On the other hand, if gains in output rather than total output are considered, then the order is probably rather different. From this point of view, the fields of heredity and environment, sensation and perception, and social behavior appear to be much more vigorous than they do when considered from the standpoint of total volume alone.

In the second place, we may point to a number of basic orientations that cut across the six areas with which we have dealt separately and that represent convergences of seemingly diverse interests. These are as follows:

1. *Emphasis on external determinants of behavior.* This emphasis shows up clearly in the ethological work on stimulus releasers, experimentation on exploratory and manipulatory behavior and curiosity, work on the effects of early environmental stimulation, and on such topics as homing, navigation, and echolocation. Perhaps complementing this trend is an interest in the field of learning and motivation, in the role of stimulation increase rather than stimulation reduction.

2. *Emphasis on influence of early environmental experience.* This represents a major trend. It appears in a number of different lines of research, including work on drives and motives, emotion, instincts, and social behavior. Although a great deal of empirical study has been devoted to the topic, few theoretical models specific to the problem have so far been formulated.

3. *Emphasis on genetic determinants of behavior.* As we have already remarked, the field of psychogenetics appears to be commanding increasing interest. Ramifications of this interest are evident in research on drives and motivation, social behavior, sensation and perception, and emotion. It seems likely that in the not too distant future, work arising from this orientation may contribute in an important way to our under-

standing of at least two basic problems, namely, the taxonomy of behavior and the phylogeny of behavior.

4. *Emphasis on study of complex, multiple responses.* This is included with some hesitation. However, the growing interest in work along ethological lines, as well as in the study of such complex processes as learning sets, multiple discriminations, and exploratory behavior seems to represent such a trend. Along with this there is a slight tendency to place some reliance on a broad naturalistic description of behavior in addition to tightly controlled laboratory experimentation.

5. *Emphasis on study of biochemical bases of behavior.* This is largely a methodological trend. It appears in work in almost all the areas which we have discussed. It is particularly prominent in research on learning, motivation, and psychogenetics. There seems little doubt that major break-throughs will be made very soon along biochemical lines and that "psychopharmacology" will rapidly become a well-defined unit of study in the general field.

It is difficult to say, in general, just what the above trends add up to. Certainly they all appear to be very different from each other at first sight. At the same time, they do interlock in a complex manner. Psychogeneticists, for example, are using biochemical methods; researchers interested in exploratory behavior are looking at early environmental influences; biochemically oriented workers studying hormonal processes underlying motivated behavior also take cognizance of external determinants of drive. Many other such instances could be mentioned. From this point of view, we may say that the above trends together suggest that the field of animal psychology has considerable unity and vitality. There is little evidence of insularity of approach or viewpoint. It is true that the key problem in the field—a problem that is central whenever the comparative approach is involved—namely, that of classification, has not yet been satisfactorily explicated. But there are strong indications of interest in this direction, so that we may hope for some of the answers before long.

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